

EXPANSION OF THE ASIATIC GREEN ALGA *CODIUM*  
*FRAGILE* SUBSP. *TOMENTOSOIDES* IN THE  
GULF OF MAINE

ARTHUR C. MATHIESON

Department of Plant Biology and Jackson Estuarine Laboratory,  
University of New Hampshire, Durham, NH 03824  
e-mail: arthur@hopper.unh.edu

CLINTON J. DAWES

Department of Biology, University of South Florida, Tampa, FL 33620

LARRY G. HARRIS

Department of Zoology, University of New Hampshire, Durham, NH 03824

EDWARD J. HEHRE

Department of Plant Biology and Jackson Estuarine Laboratory,  
University of New Hampshire, Durham, NH 03824

**ABSTRACT.** The invasive Asiatic green alga *Codium fragile* subsp. *tomentosoides*, which was introduced to the northwestern Atlantic in eastern Long Island Sound, New York during 1957, has recently colonized several parts of the Gulf of Maine via two invasion sites: (1) mid-coastal Maine at Boothbay Harbor after transplantation of Long Island oysters (1964); and (2) southern Massachusetts as a result of the expansion of attached plants from the Cape Cod Canal (1969) into nearby Cape Cod Bay (1972). Because of its warm-water affinities, southern New England populations initially expanded more rapidly than northern ones, becoming particularly invasive in shallow subtidal habitats. By contrast, the Boothbay Harbor populations were rather “quiescent,” long-lived, and circumscribed until the early 1970s. After a buildup of significant biomass, extensive fragmentation and drifting occurred via strong south-flowing currents; thereafter, *Codium* colonized mid-coastal Maine, New Hampshire, and northern Massachusetts. Currently, the Casco Bay area just south of Boothbay Harbor has the highest number of invasion sites, particularly at offshore islands. Attached populations are limited to a few contiguous sites just north of Boothbay Harbor, with only drift specimens occurring in “Downeast” Maine. Recent introductions have also been recorded in the Canadian Maritime Provinces, both within the Atlantic (1989) and the Gulf of St. Lawrence (1996) shorelines. Thus, the species’ expansion in the northwestern Atlantic has involved multiple introductions, different vectors (shellfish and vessels), dispersal by major south-flowing currents, and differential viability/abundance of *in situ* populations due to varying hydrographic and exposure conditions. In comparing a series of permanent study sites in southern Maine and New Hampshire during 1982 to 2001, *Codium* increased from one to 26 sites during 19 years, with the most evident expan-



sion between 1996–1998. A comparison of several demographic features (length, weight, density, biomass, and percent occurrence) for six *Codium* populations ranging from mid-coastal Maine to New Hampshire showed that outer estuarine and nearshore open coastal plants were smaller and had more limited densities and biomass than those found at warmer offshore insular sites like Star Island, New Hampshire. *Codium* is now the dominant canopy species in some southern Maine and New Hampshire locations, extending to ~8 m below mean low water; it occurs in both disturbed sites (e.g., former urchin barrens) and established kelp beds at sheltered and exposed locations. The Asiatic red alga *Neosiphonia* (= *Polysiphonia*) *harveyi*, which is the dominant epiphyte on *Codium*, is also exhibiting a rapid expansion in this same geography. Drifting populations of *Codium* may be a good vector for its introduction, as well as for several other epiphytes. Another aspect of the invasion of *Codium* into the Gulf of Maine is the spread of the introduced bryozoan *Membranipora membranacea*, which is common on kelps but appears to be exhibiting enhanced survival on *Codium* because of its perennial growth pattern and lack of epibiontic sloughing.

**Key Words:** green alga, Chlorophyta, *Codium fragile* subsp. *tomentosoides*, Asiatic, introduced, nonindigenous, invasive, Gulf of Maine, dispersal, distribution, ecology, epiphytes

Introduced species are a major problem throughout the world's oceans, causing altered natural communities and significant economic losses (Boudouresque et al. 1994; Carlton 1979, 1996, 2000; De Clerk et al. 2002; Chapman et al. in press; Jousson et al. 2000; Karlsson and Loo 1999; Lein 1999; Maggs and Stegena 1999; Meinesz 1999; Meinesz et al. 1993; Pederson 2000; Piazzzi and Cinelli 2000; Ramus 1971; Reise 1999; Rueness and Rueness 2000; Stiger and Payri 1999; Thresher 2000). In the northwestern Atlantic ten nonindigenous seaweeds are known (cf. Broom et al. 2002; Coll and Cox 1977; Humm 1979; Kjellman 1897; McIvor et al. 2000, 2001; Sears 2002; Taylor 1962; Villalard-Bohnsack 2002; Vitousek et al. 1996): the invasive green alga *Codium fragile* (Suringar) Har. subsp. *tomentosoides* (Goor) P. C. Silva (hereafter *Codium*); the brown algae *Colpomenia peregrina* Sauv. and *Fucus serratus* L.; and the red algae *Antithamnion pectinatum* (Mont.) Brauner, *Bonnemaisonia hamifera* Har. [including the "*Trailliella intricata*" (J. Agardh) Batters stage], *Furcellaria lumbricalis* (Huds.) J. V. Lamour., *Grateloupia turuturu* Yamada [= *G. doryphora* (Mont.) M. Howe; cf. Gavio and Fredericq 2002], *Lomentaria clavellosa* (Turner) Gaillon, *Neosiphonia* (= *Polysiphonia*) *harveyi* (Bailey) Kim, Choi, Guiry & G. W. Saun-



ders, and *Porphyra suborbiculata* Kjellm. (= *P. carolinensis* Coll & J. Cox; cf. Broom et al. 2002). *Bonnemaisonia hamifera*, *Codium*, *N. harveyi*, and *P. suborbiculata* are Asiatic, while the rest are from Europe, the Pacific, or unknown locations (Blackler 1964; Coleman 1996; Dale 1982; Foertch et al. 1991; Goff et al. 1992; Harvey 1853; Kjellman 1897; Lewis and Taylor 1928, 1933; Marston and Villalard-Bohnsack 2000; McIvor et al. 2000, 2001; Silva 1955, 1957; Villalard-Bohnsack 2002; Wilce and Lee 1964). The earliest documented introductions within this geography date back to the early to late 1800s and include *F. serratus* from the Canadian Maritime Provinces (Dale 1982; Hay and Mackay 1887; Novaczek 2001; Robinson 1903), *F. lumbricalis* from Newfoundland (Harvey 1853; Novaczek 2001), and *N. harveyi* from Connecticut (Harvey 1853; McIvor et al. 2000, 2001); most recently, the foliose red alga *G. turuturu* was recorded from Rhode Island (Marston and Villalard-Bohnsack 2000; Villalard-Bohnsack and Harlin 1997). Of these ten seaweeds, *Bonnemaisonia* is persistent and broadly distributed; *Codium*, *Grateloupia*, and *N. harveyi* are rapidly expanding; *C. peregrina* is restricted to a few locations; and the others exhibit limited expansions (Bird and Edelstein 1978; Blackler 1964; Broom et al. 2002; Carlton and Scanlon 1985; Marston and Villalard-Bohnsack 2000; McIvor et al. 2000, 2001; Sears 2002; South and Tittley 1986; Villalard-Bohnsack 2002). The Asiatic red alga *Porphyra yezoensis* Ueda (i.e., nori) has recently been cultivated within “Downeast” Maine and New Brunswick, Canada but has shown no signs of escaping or becoming invasive (Watson et al. 1998, 2000).

Trowbridge (1995, 1996, 1998) has described the introduction and spread of several seaweeds throughout the world that show varying patterns. After escaping from a coastal aquarium, the tropical/subtropical green alga *Caulerpa taxifolia* (Vahl) C. Agardh has become a major pest within the Mediterranean (Boudouresque et al. 1994; Meinesz 1999; Meinesz et al. 1993; Raloff 1998; Wiedenmann et al. 2001), as well as being recently found in California (Jousson et al. 2000). Vectors for other seaweed introductions include: Lessepsian migrations into the Mediterranean via the Suez Canal, shellfish/algal transplants, mariculture introductions, and accidental transfers via ballast water, anchors, fishing nets, ships’ hulls, oil platforms, and shellfish packaging (Aleem 1948, 1992; Carlton 1987; De Clerk et al. 2002; Hay



1990; Loosanoff 1975; Maggs and Hommersand 1993; Modena et al. 2000; Moss et al. 1981; Piazzzi et al. 1997; Russell 1982, 1983; Scagel 1956; Verlaque 1994). The temperate brown algae *Laminaria japonica* Kjellm., *Sargassum muticum* (Yendo) Fensholt, and *Undaria pinnatifida* (Harv.) Suringar have spread dramatically during the last century, extending between different ocean basins and hemispheres (Cecere et al. 2000; Critchley et al. 1983, 1990; Floc'h et al. 1991; Hay 1990; Hay and Villouta 1993; Karlsson and Loo 1999; Rueness 1989; Sanderson 1990; Scagel 1956; Staehr et al. 2000; Trowbridge 1995, 1996). Their dispersal is attributable in large part to shipping and oyster importation activities. *Sargassum*, like *Codium* (see below), has become an ecological and economic pest, disrupting oyster beds, boat harbors, etc. (Rueness 1989). By contrast at least 95 introduced seaweeds are more localized (Farnham 1980; Verlaque 1994), with some producing naturalized and viable populations (Russell 1983, 1992; Russell and Balazs 1994).

The invasive Asiatic green alga *Codium fragile* subsp. *tomentosoides* is commonly called "sputnik weed" or "oyster thief" because of its rapid growth, as well as its ability to attach, uplift, and transport shellfish (Hanisak 1980; Novaczek 2001). The first record of foreign travel by *Codium* dates back to ~1900 in Holland, where it was presumably introduced with shellfish (Silva 1955, 1957; van Goor 1923). Thereafter it expanded rapidly in Europe, extending from Norway to Spain into the western edge of the Mediterranean (Jones 1974; Lüning 1990; Meslin 1964; Parriaud 1957; Silva 1955; Trowbridge and Todd 1999, 2001). *Codium* was first recorded in 1957 from the northwestern Atlantic in eastern Long Island Sound (Bouck and Morgan 1957). Other recent introductions have occurred in Australia, New Zealand, the central Pacific Islands, Japan, Alaska to Pacific Mexico, and western South America (Lüning 1990; Nelson 1999; Trowbridge 1995, 1996, 1998). Carlton and Scanlon (1985) considered three possible vectors for the transoceanic dispersal of *Codium* to the northwestern Atlantic: (1) fouling of the flat oyster *Ostrea edulis* L. from Europe; (2) fouling of the Pacific or Japanese oyster *Crassostrea gigas* (Thunb.) from Washington and British Columbia; and (3) fouling of ships' hulls from Europe. They concluded that it was most likely transported as a fouling organism on ships' hulls (cf. Loosanoff 1975; Malinowski 1974), as there was daily shipping between Europe and New York during the mid-1950s



just prior to the discovery of *Codium* (Bouck and Morgan 1957). Dromgoole (1975, 1979) stated that *Codium* has several features that would preadapt it for ship-borne dispersal: (1) settlement on floating structures imperfectly coated with antifouling paint; (2) attachment to diverse substrata with minimal relief; and (3) regeneration from residual holdfasts subjected to reduced shear stress during ship-borne dispersal (Hanisak 1980). Carlton and Scanlon (1985) suggested a fourth factor that would be critically important, namely the species' physiological plasticity, which would permit it to exist through broad and changing temperature and salinity regimes. They suggested that the species' localized dispersal was largely caused by currents, transport of fishery products, and other natural mechanisms. For example, the initial establishment of *Codium* on the south shore of Massachusetts (MA) during 1961 and at Boothbay Harbor, Maine (ME) in 1964 probably occurred after transfer of juvenile/microscopic plants (i.e., "green bumps") on oysters (Coffin and Stickney 1966; Galstoff 1962a,b; Malinowski 1974; Wood 1962). Other possibilities include transport of plants on boat propellers, the cutting off of *Codium* thalli from shellfish (oysters) and tossing them back into the water, entrainment on commercial drag nets, and dispersal via packing material for lobsters, bait worms, etc. (Carlton 1979; Dawson and Foster 1982; Garbary et al. 1997; Hillson 1976; Novaczek 2001; Orris 1980). Aside from human causes, natural dispersal mechanisms may include motile reproductive cells, vegetative fragments, and floatation of whole plants via currents.

*Codium* populations within the northwestern Atlantic, like those in Europe, have expanded rapidly and now extend from the Canadian Maritime Provinces (i.e., Nova Scotia, New Brunswick, and Prince Edward Island) to North Carolina (Bird et al. 1993; Bleakney 1996; Chapman 1999; Chapman et al. in press; Coleman and Mathieson 1974; Davis 1971; Garbary and Jess 2000; Garbary et al. 1997; Hubbard and Garbary 2001, 2002; Meimer 1972; Scheibling 2001; Schneider and Searles 1991; Schumacher and Fiore 1963; Searles et al. 1984; Sisson 1968; Taylor 1967; Wassman and Ramus 1973a,b). Currently it dominates many subtidal habitats in the Canadian Maritime Provinces and New England, replacing *Laminaria* as the major taxon, and often impacting shellfish communities (Berman et al. 1992; Carlton and Scanlon 1985; Hanisak 1980; Harris and Mathieson 2000; Harris and Tyrrell 2001; Hulbert 1980; Lüning 1990; Martin et al. 1988; Ramus



1971; Scheibling 2001; Tacy et al. 1977; Van Patten 1992). In contrast to New England and the Canadian Maritime Provinces where *Codium* is often a subtidal pest (Coleman 1996; Garbary et al. 1997; Hubbard and Garbary 2001, 2002; Prince 1987), it is less abundant in Europe and New Zealand, often producing small distinct intertidal populations (Bartsch and Kuhlenkamp 2000; Chapman 1999; Chapman et al. 2001; Freeman and Smith 2000). In New England, *Codium* is more abundant south than north of Cape Cod, MA, presumably because of its warm-temperate affinities and the occurrence of a major phytogeographic boundary at Cape Cod (Carlton and Scanlon 1985; Fralick and Mathieson 1973; Hanisak 1980; Hutchins 1947; Lüning 1990; Mathieson et al. 1991; Ramus 1971). The goal of this paper is to review the recent rapid spread of *Codium* within the Gulf of Maine (Figure 1), which extends from the mouth of the Bay of Fundy southward to Cape Cod, MA. We will use a combination of historical and recent studies, including extensive collections and quantitative sampling, to describe the plant's current status. Among others, Davis et al. (2001) have emphasized the importance of comparing historical and present-day collections in understanding the temporal occurrences of marine biota.

#### MATERIALS AND METHODS

The distribution of *Codium* throughout the Gulf of Maine is summarized based upon ten previous floristic studies conducted between 1965 and 2001 (Mathieson 1979; Mathieson et al. 1993, 1996, 1998, 2001; Mathieson and Fralick 1972; Mathieson and Hehre 1986; Mathieson and Penniman 1986a,b, 1991), including several unpublished studies (Mathieson and Hehre). That is, seasonal collections of all conspicuous seaweeds were taken within the intertidal (on foot) and subtidal zones (by SCUBA) at 922 sites within Maine, New Hampshire (NH) and Massachusetts. A variety of taxonomic references were employed for the identification of various epiphyte populations (cf. Mathieson et al. 1998, 2001). Nomenclature primarily follows South and Tittley (1986) and Sears (2002), except for some recent changes noted by Broom et al. (2002), Choi et al. (2001), Gavio and Fredericq (2002), and Maggs et al. (2002). Voucher specimens of all *Codium* populations were prepared and deposited in the Albion R.



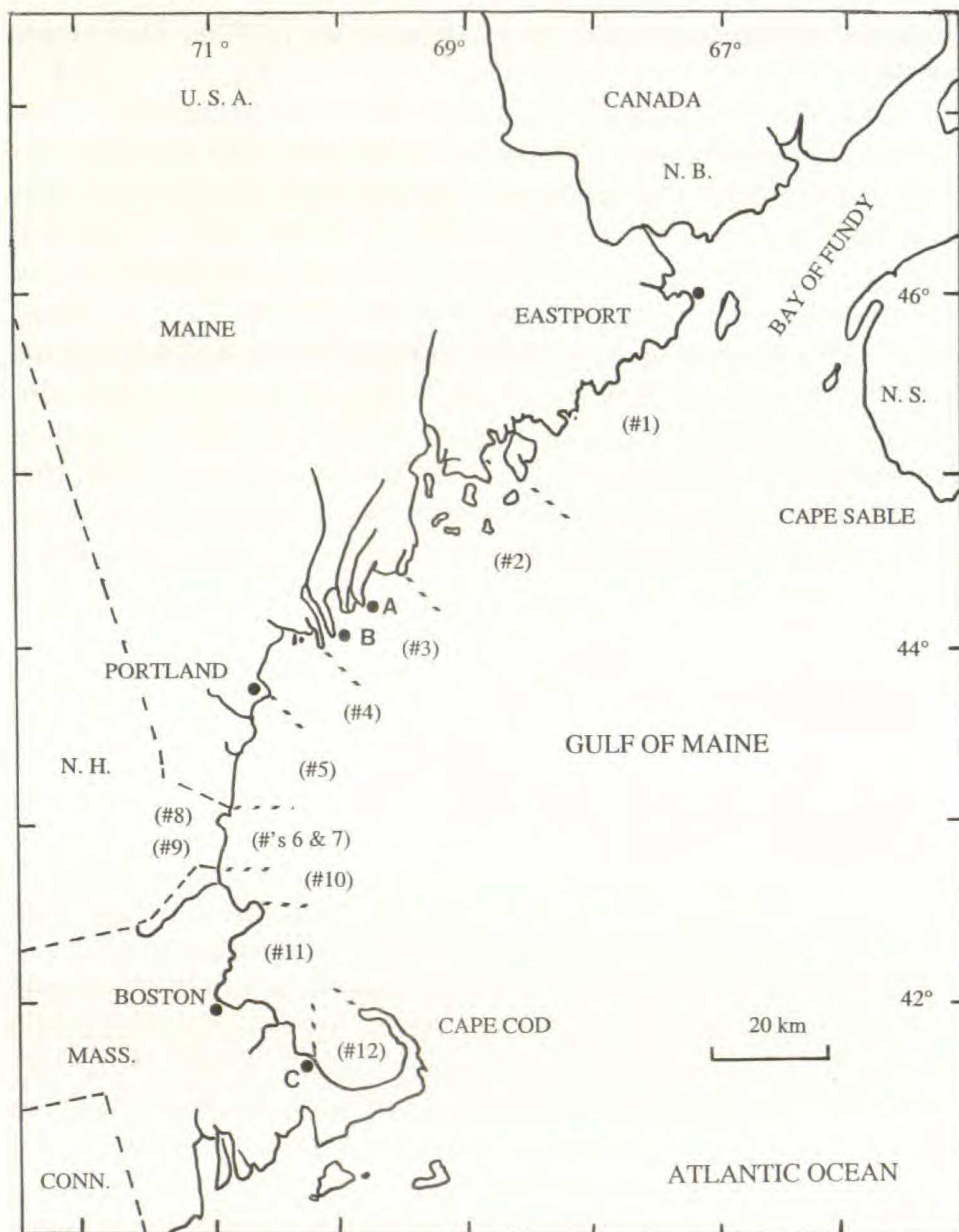


Figure 1. The northwestern Atlantic coastline from Nova Scotia, Canada to Cape Cod, including the northern invasion site for *Codium* at Boothbay Harbor, ME ("A"), a study site at Jaquish Island, ME ("B"), its southern invasion site near the mouth of the Cape Cod Canal and Cape Cod Bay ("C"), plus twelve major habitats within the Gulf of Maine: #1 "Down East" ME; #2 Penobscot Bay, ME; #3 the "Indented Coastline" of ME; #4 Casco Bay, ME; #5 the southern ME coastline; #6 the NH/ME Isles of Shoals; #7 the NH nearshore open coast; #8 the NH/ME Great Bay Estuarine System; #9 the NH Hampton-Seabrook Estuarine System; #10 the "North Shore" of MA, or Salisbury to Gloucester, MA; #11 Salem to Sagamore, MA; #12 the Cape Cod peninsula, or Sandwich to Provincetown, MA. Abbreviations: MASS. = Massachusetts; N.B. = New Brunswick, Canada; N.H. = New Hampshire; N.S. = Nova Scotia, Canada.



Hodgdon Herbarium (NHA) of the University of New Hampshire (UNH).

Of the 922 total sites investigated, 68% were in Maine, ~25% in New Hampshire, and ~7% in Massachusetts. The presence and relative abundance (% occurrence) of epiphytic populations, plus their host populations, were enumerated based upon a subsampling of 150 herbarium voucher specimens (Appendix) from twelve contiguous Gulf of Maine habitats (Figure 1): (1) "Downeast" ME, extending from Mount Desert Island eastward to the Canadian border; (2) Penobscot Bay (ME), the state's largest embayment, extending from the mouth of the Penobscot River at Searsport to St. George; (3) the "Indented Coastline" (ME) that extends from St. George to Brunswick and consists of a series of eroded peninsulas and river drainage areas; (4) Casco Bay (ME) near Portland, the state's second largest embayment that extends from Phippsburg to Cape Elizabeth; (5) the southern ME coastline from Cape Elizabeth to Kittery near the NH border; (6) Isles of Shoals, an archipelago of nine offshore islands within ME and NH; (7) the NH nearshore open coast; (8) the NH/ME Great Bay Estuarine System; (9) the NH Hampton Seabrook Estuarine System; (10) the North Shore of Massachusetts, extending from Salisbury to Gloucester; (11) the MA shoreline extending from Salem to Sagamore; (12) the northern shoreline of the Cape Cod peninsula extending from Sandwich to Provincetown (MA).

The temporal invasion by *Codium* of the southern ME and NH coastline between Bald Head Cliff, York, ME and Seabrook, NH (Figure 2) is summarized based upon a subset of 276 of the 922 total sites. The locations include nine offshore NH/ME islands at the Isles of Shoals (Mathieson and Hehre 1986; Mathieson and Penniman 1986a), 17 nearshore open coastal NH/ME locations (Mathieson and Hehre 1986; Mathieson et al. 2001), 20 ME sites within the York River Estuary (Mathieson et al. 1993), 44 ME sites within Brave Boat Harbor (Mathieson et al. 2001), 137 NH/ME sites within the Great Bay Estuarine System (Mathieson and Hehre 1986; Mathieson and Penniman 1986b), and 49 NH locations within the Hampton-Seabrook Estuarine System (Mathieson and Fralick 1972).

Detailed ecological studies have been conducted by L. Harris and students at Star Island, NH Isles of Shoals (Figure 2) since 1974 and at five other Shoals sites since 1992 (Berman et al. 1992; Harris et al. 1994, 1996; Harris and Chester 1996; Harris



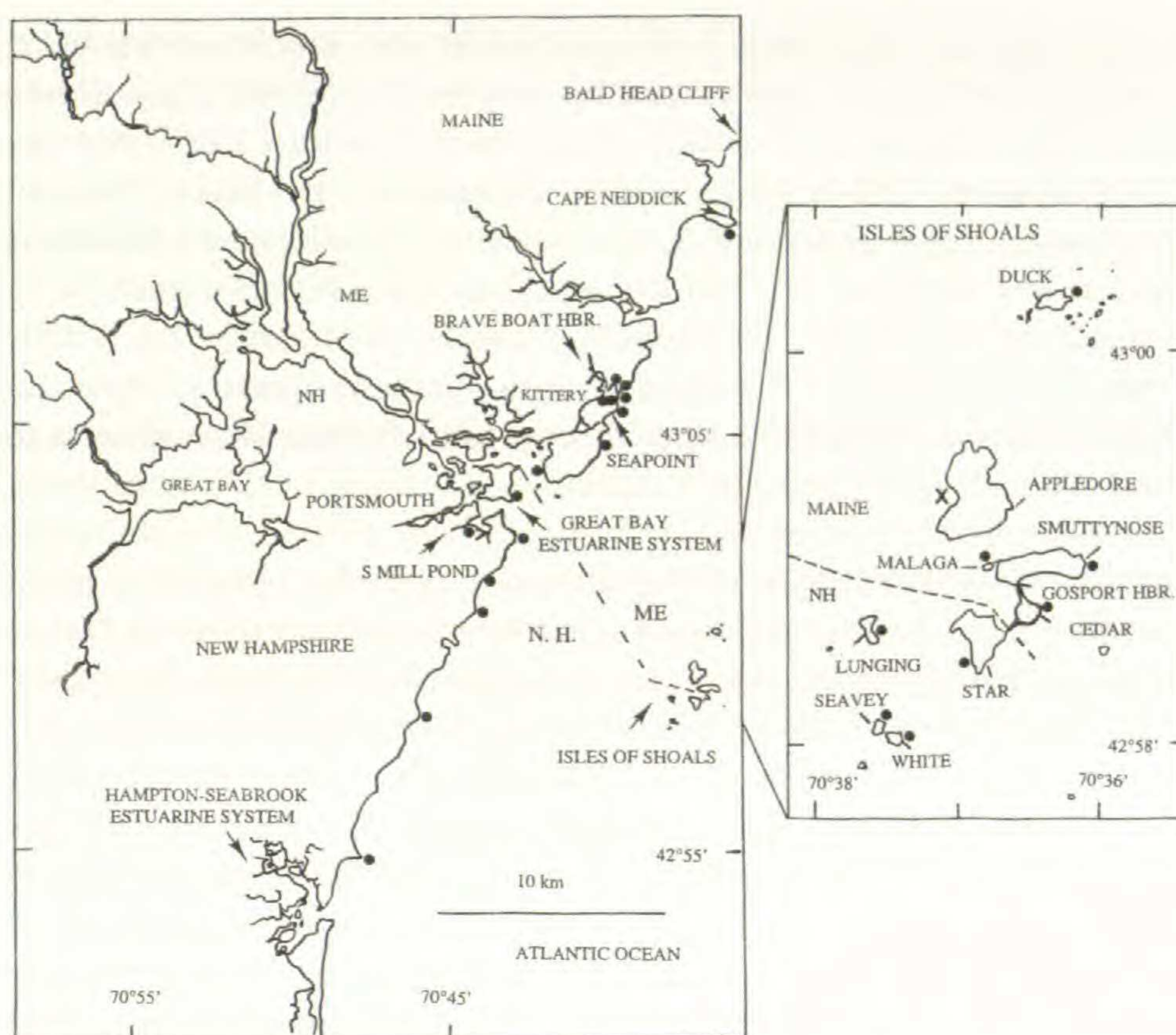


Figure 2. Locations of attached *Codium* populations on the southern Maine and New Hampshire coastlines during 1983 and 2001; the enlarged area on the right shows the Isles of Shoals, an archipelago of nine interstate islands. Symbols: X = initial occurrence in 1983, as well as during 2001; black circles = occurrences in 2001. Five of the six study sites for *Codium* populations are also shown with arrows (lines): Cape Neddick, Brave Boat Harbor, and Seapoint, ME, plus South Mill Pond and Star Island, NH. The location of the Jaquish Island study site is shown in Figure 1.

and Tyrrell 2001; Hulbert 1980; Martin et al. 1988; Tacy et al. 1977; Witman 1984, 1985, 1987; Witman et al. 1982). These studies have provided a general understanding of the changing patterns of diverse benthic organisms, including several native seaweeds (*Agarum clathratum* Dumort., *Chondrus crispus* Stackh., *Laminaria* spp., and *Ptilora serrata* Kütz.) and the green sea urchin *Strongylocentrotus droebachiensis* (Müller), plus the invasive, introduced green alga *Codium* and the non-native bryozoan *Membranipora membranacea* (L.). Upper horizontal rocky substrata were studied at all six Shoals sites, which have historically either been dominated by large algal canopies (e.g., *Lam-*



*inaria* spp.) or, if destructively grazed by sea urchins, they have consisted of barrens dominated by crustose coralline algae (Hulbert 1980; Martin et al. 1988; Ojeda and Dearborn 1989; Sebens 1985; Witman 1984, 1985, 1987; Witman et al. 1982). Patterns of canopy, algal distribution, and relative abundance of different taxa at five of these six NH Shoals sites (i.e., White Island #1 & 2, Lunging Island #3, Star Island #4 & 5; cf. Harris et al. 1994, 1998) are compared. A Nikonos V underwater camera, outfitted with a flash, 15 mm lens, and 35 mm Ektachrome slide film, was used to document changes in relative abundance and community structure from  $\sim +3.0$  to  $-12$  m relative to mean low water (MLW). Counts of canopy species were made by projecting these pictures on a screen and documenting relative abundance based upon 30 photographs per site (cf. Harris and Mathieson 2000). Data for *Codium* and the brown alga *Desmarestia aculeata* (L.) J. V. Lamour. are probably an underestimate since neither small nor individual plants could be distinguished. By contrast, the single blades of the brown algae *A. clathratum* and *Laminaria* spp. are more accurately represented. Subtidal canopy populations of *C. fragile* subsp. *tomentosoides*, *A. clathratum*, and *L. saccharina* at Star Island were sampled ( $-4$  to  $-15$  m) just prior to the spring recruitment of the bryozoan *M. membranacea* (June 2000) in order to assess patterns of host specificity.

A series of permanent transect studies have been conducted annually by students at the Shoals Marine Laboratory, with these documenting percent coverage of the dominant intertidal organisms on Star Island, NH from 1965–1972 (cf. Kingsbury 1976) and on Appledore Island, ME from 1973 to the present. Ten years of intertidal transect data on Appledore (Figure 2) were evaluated to confirm the initial establishment of *Codium* during 1986–1995, with the data being supplied by present (Dr. Jim Morin, Director) and former Shoals Marine Laboratory personnel (Drs. Sarah Cohen and Michael Lesser). Twenty-eight transects are located around the perimeter of Appledore Island, with these ranging from fully exposed to very sheltered locations. Four sheltered transects with *Codium* populations were compared, with their locations (directions) relative to magnetic north being as follows: T2 (W shore at  $250^\circ$  and in Babb's Cove), T5 (W shore at  $242^\circ$ ), T24 (SE shore at  $159^\circ$ ), and T28 (SW shore at  $230^\circ$ ). Data from earlier floristic surveys of the Shoals (Mathieson and Hehre 1986; Mathieson and Penniman 1986a) also served as a baseline to



compare the initial occurrence of *Codium*; these were supplemented in 1994 by Ms. Amy Cook (a former UNH undergraduate) who documented the species' potential occurrence on all nine islands (Figure 2). Voucher specimens of her collections are deposited in NHA.

Several demographic features of *Codium* populations at six sites from mid-coastal ME to NH (Figures 1 and 2) were studied in order to compare geographical patterns of colonization, abundance, and physiological optima under variable hydrographic conditions. The six sites included: an insular NH site at Star Island, Isles of Shoals; a Maine nearshore open coastal location at Jaquish Island near the Boothbay Harbor invasion site at the Commercial Fisheries Biological Laboratory, plus Cape Neddick, York and Seapoint, Kittery; and two outer estuarine sites, one in Brave Boat Harbor, York/Kittery, ME, and the other in South Mill Pond, Portsmouth, NH. Mean frond length (cm), damp-dried weight (g), density (no./m<sup>2</sup>), biomass (g/m<sup>2</sup>), and percent occurrence were enumerated for each location, except Cape Neddick where no destructive sampling for weight and biomass was taken due to the plant's low density in a permanent study site (cf. Chavanich and Harris 2000). The above measurements were based upon a sampling of 25–30 randomly tossed quadrats (0.1 m<sup>2</sup>). As plants at Brave Boat Harbor, ME are restricted to the perimeter of relatively deep salt marsh pannes, area-based density and biomass estimates at this site are not directly comparable to the other five sites. Therefore, linear- (i.e., perimeter) and area-based assessments of density and biomass at Brave Boat Harbor are given.

A comparison of surface water temperatures at an insular (Isles of Shoals, NH/ME) and a contiguous nearshore open coastal site (Cape Neddick, ME) within the Gulf of Maine (Figure 2) was made during the summers of 2000 and 2001 (i.e., June–September). The data, which were collected from the web site <http://marine.rutgers.edu/mrs> after imputing corresponding latitude and longitude values, showed variable color codings and surface water temperatures (°C). Usable images (i.e., data) were available only if both sites were simultaneously visible and if measurements were made between a 6:00–10:00 am period.

## RESULTS

**Insular and nearshore surface water temperatures.** Figure 3 shows a comparison of mean weekly surface water temperatures



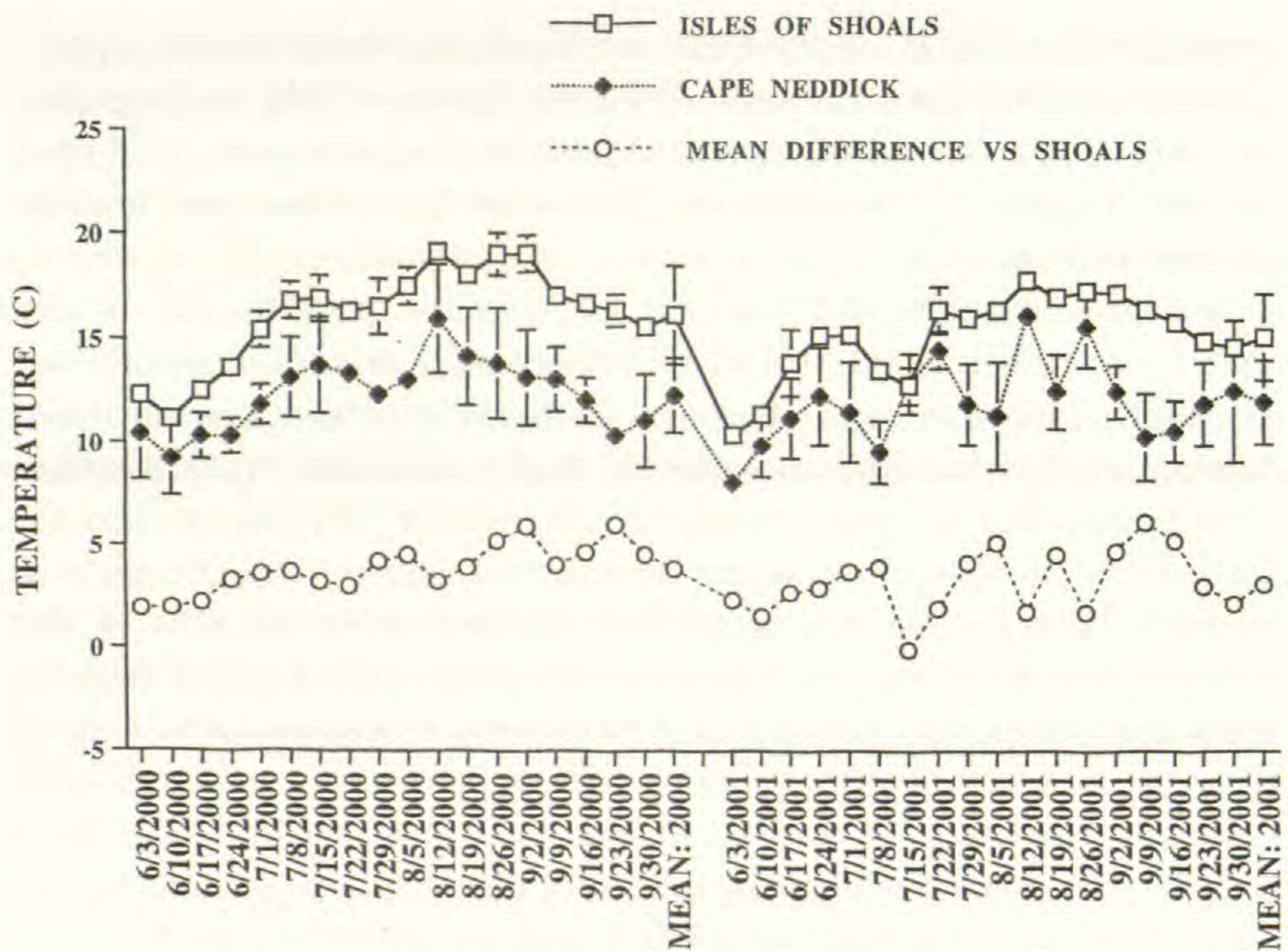


Figure 3. A comparison of surface water temperatures at the Isles of Shoals, NH/ME and Cape Neddick, ME during the summers of 2000 and 2001 (i.e., June–September), with the data being based upon satellite imagery and expressed as mean weekly temperatures ( $\pm$  SD). A synopsis of mean weekly differences between sites is also shown.

( $\pm$  SD) at the Isles of Shoals, NH/ME (insular) and Cape Neddick, ME (nearshore) during two consecutive summers, plus mean differences versus the Shoals (i.e., + or –). The insular (i.e., Shoals) site was consistently warmer than Cape Neddick (i.e., +1.7 to 6.1°C), except during one week in early July, 2001 (i.e., –0.1°C). Mean values for both sites also showed a conspicuous difference, with those at the Shoals during 2000 being  $16.1 \pm 2.3^\circ\text{C}$  versus  $12.1 \pm 1.8^\circ\text{C}$  at Cape Neddick; the corresponding values for 2001 were  $15.0 \pm 2.1^\circ\text{C}$  and  $11.9 \pm 2.0^\circ\text{C}$ , respectively.

**Present distribution of *Codium* within the Gulf of Maine.** Figure 4A illustrates the occurrence of attached (Figure 5A–5D) and drift plants of *Codium* (Figure 5E–5H) within the Gulf of Maine, expressed as the number of collection sites within twelve contiguous habitats ranging from “Downeast” ME to Provincetown, MA. The numbers of identifiable epiphyte taxa are also



shown in Figure 4B. Only drift specimens of *Codium*, composed of small fragments or larger proliferous fronds (Figure 5E–5H), are known from “Downeast” ME, plus the Great Bay (ME/NH) and Hampton-Seabrook (NH) Estuarine Systems. No populations (drift or attached) are known from Penobscot Bay (ME); further south, attached populations are recorded at 12 sites within Maine’s “Indented Coastline,” at 21 Casco Bay, ME sites, 15 southern ME nearshore sites (including outermost Brave Boat Harbor), nine islands within the NH/ME Isles of Shoals, seven NH nearshore open coastal sites (including outermost Portsmouth Harbor), one “North Shore” MA site, and at four sites each between Salem and Sagamore, MA, and Sandwich and Provincetown, MA. Two major patterns are evident: (1) a prevalence of sites downstream from the initial 1964 introduction at Boothbay Harbor, ME; and (2) a reduced and clinal decrease from Provincetown to the “North Shore” of MA, which is northward of a second invasion site via the Cape Cod Canal (1969–1972). As shown in the Appendix, *Codium* has a restricted contiguous distribution north of Boothbay Harbor, only occurring at Bristol and South Bristol, ME.

**Chronological occurrence and invasion of *Codium* within southern Maine and New Hampshire.** The invasion of southern ME and NH by *Codium* between 1982 and 2001 is summarized in Figure 6 and Table 1. Drift specimens (Figure 5E–5H) were often found prior to attached populations (Table 1). For example, at the Isles of Shoals (Figure 2) drift samples were initially observed at Appledore Island, ME during 1982, followed by attached populations one year later within Babb’s Cove and contiguous sheltered sites on the same island. By 1986, *Codium* had formed dense subtidal beds in many sheltered Appledore sites, as well as expanded into the sheltered Gosport Harbor side of Smuttynose Island, ME. Two years later, student transect studies on Appledore (Table 2) documented an initial 6–12% coverage in the low intertidal at three sheltered sites (T2, T5, and T24), increasing to 15 and 12% on two transects (T2 and T24) during 1995. *Codium* was well established on the exposed side of Appledore during 1993 (Table 1). A floristic survey in 1994 showed its presence on Appledore, Duck, Malaga, and Smuttynose Islands, ME, plus Lunging, Seavey, and White Islands, NH. In 1995



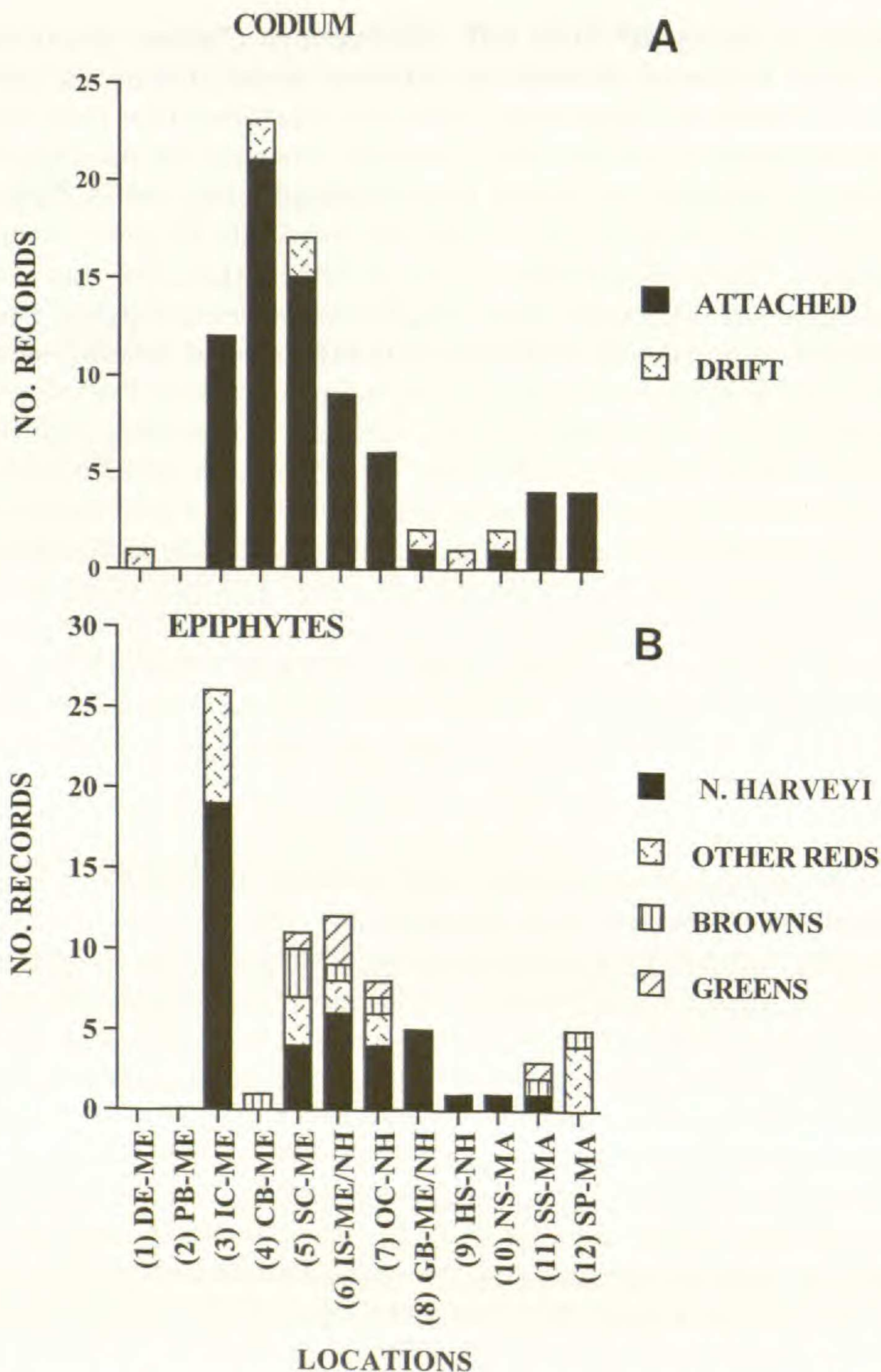


Figure 4. The distribution of attached and drift populations of *Codium* within twelve contiguous Gulf of Maine habitats (A). The presence of the Asiatic red alga *Neosiphonia harveyi*, plus various red, brown, and green algal epiphytes, are also shown within the same habitats (B). See Figure 1 for location of the twelve sites, with these being abbreviated as follows: (1) DE-ME = "Down East" ME; (2) PB-ME = Penobscot Bay, ME; (3) IC-ME = the "Indented Coastline" of ME; (4) CB-ME = Casco Bay, ME; (5) SC-ME = the southern ME coastline; (6) IS-ME/NH = the ME/NH Isles of Shoals;



it had extended to Star Island, NH, while in 1998 it was present on Cedar Island Ledge, ME.

The temporal occurrence of *Codium* on the nearshore open coast of southern ME and NH is also summarized in Figure 6 and Table 1. Drift populations were initially recorded in 1985 at Rye Ledge, Rye, NH (42°58'20"N, 70°45'33"W). During the same year, drift populations were also found at Weeks Point, Greenland, NH (43°03'32"N, 70°51'42"W) within the inner reaches of the Great Bay Estuarine System (Table 1). Four years later (1989) attached plants were first recorded from southern ME at Cape Neddick, York (43°09'56"N, 70°35'25"W). In NH, *Codium* was first found on the nearshore open coast at Fort Stark, Newcastle (43°03'22"N, 70°42'49"W) during 1992. By 1994, it was recorded at a third nearshore site, followed by four in 1995, nine in 1997, 15 in 1998, and 16 in 2001. *Codium* was just recently found (2001) at a eutrophied outer estuarine site near Portsmouth, NH. In summary, the nearshore open coast of southern ME and NH was colonized five years later than the Shoals, with a rapid increase in number of sites between 1997 and 1998. A comparison of the situation at Rye Ledge and Weeks Point, where drift populations were found in 1985, shows that it took approximately nine years for a permanent population to become established at Rye Ledge (1994); the inner estuarine Weeks Point site was never colonized.

After its initial recording within Babb's Cove on Appledore Island, ME, *Codium* spread to 25 other sites during the next 17 years (Figure 6; Table 1). Presently, it is known from each of the nine islands at the Isles of Shoals, from 12 nearshore open coastal sites, plus four outer estuarine sites in Brave Boat Harbor, ME, and one outer estuarine site in Portsmouth Harbor, NH. Three additional drift records include Long Sands, York, ME (43°09'57"N, 70°35'26"W); Weeks Point, Greenland, NH within the inner reaches of the Great Bay Estuarine System; and Knowles Island, Hampton, NH (42°53'20"N, 70°49'24"W) within the

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←

(7) OC-NH = the NH nearshore open coast; (8) GB-ME/NH = the ME/NH Great Bay Estuarine System; (9) HS-NH = the NH Hampton-Seabrook Estuarine System; (10) NS-MA = the "North Shore" of MA, or Salisbury to Gloucester, MA; (11) SS-MA = Salem to Sagamore, MA; (12) SP-MA = the Cape Cod peninsula, or Sandwich to Provincetown, MA.



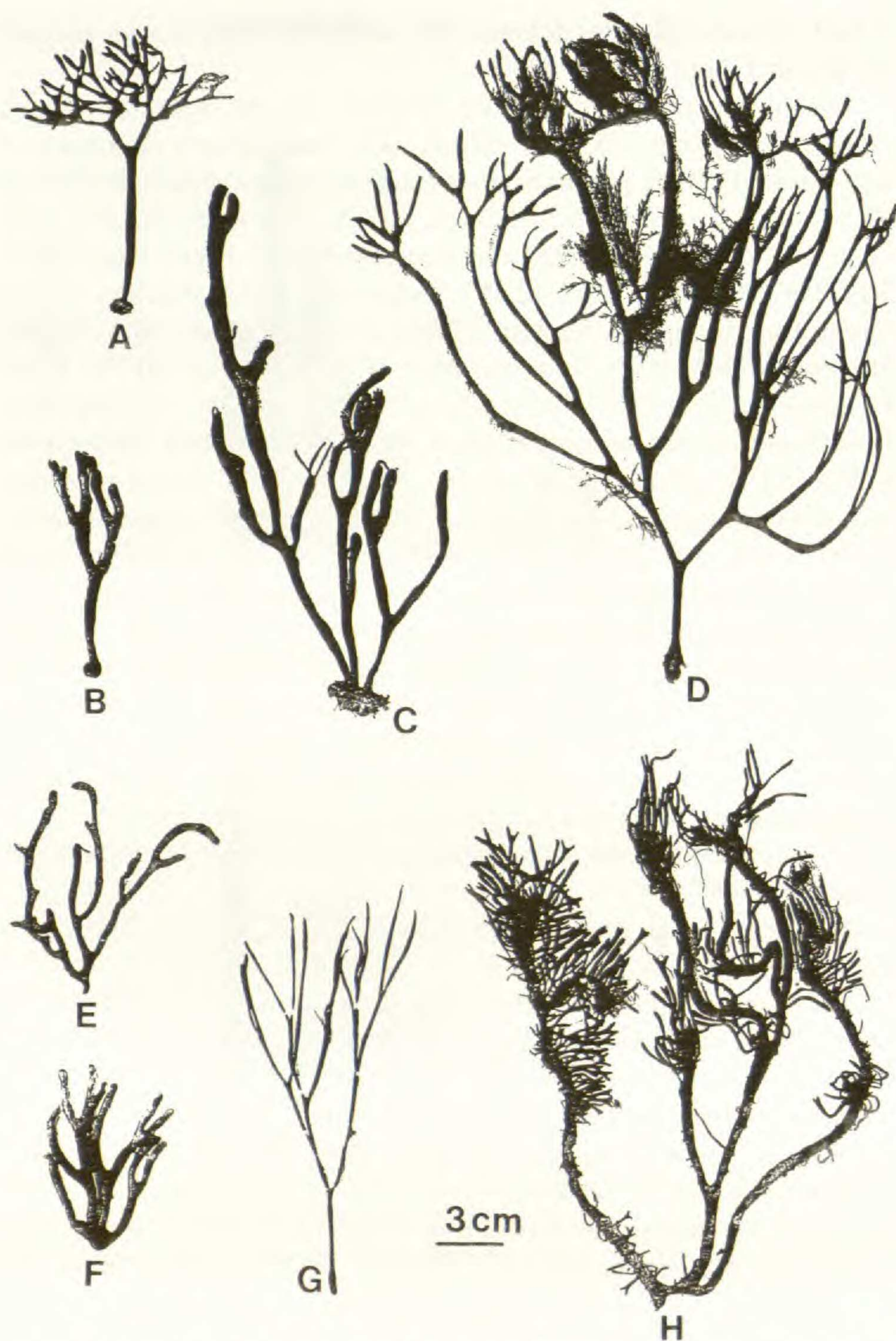


Figure 5. Morphology of attached fronds and detached fragments of *Codium*; note variability of frond stature for attached plants (A–D), including the abundance of the epiphytic red alga *Neosiphonia harveyi* (D); drift fragments (E–H) also exhibit pronounced variability of stature, segmentation, and proliferation, with some being small, thick fragments (E and F), others being constricted and having incipient “winter fragmentation” (G), or relatively large and proliferous (H).



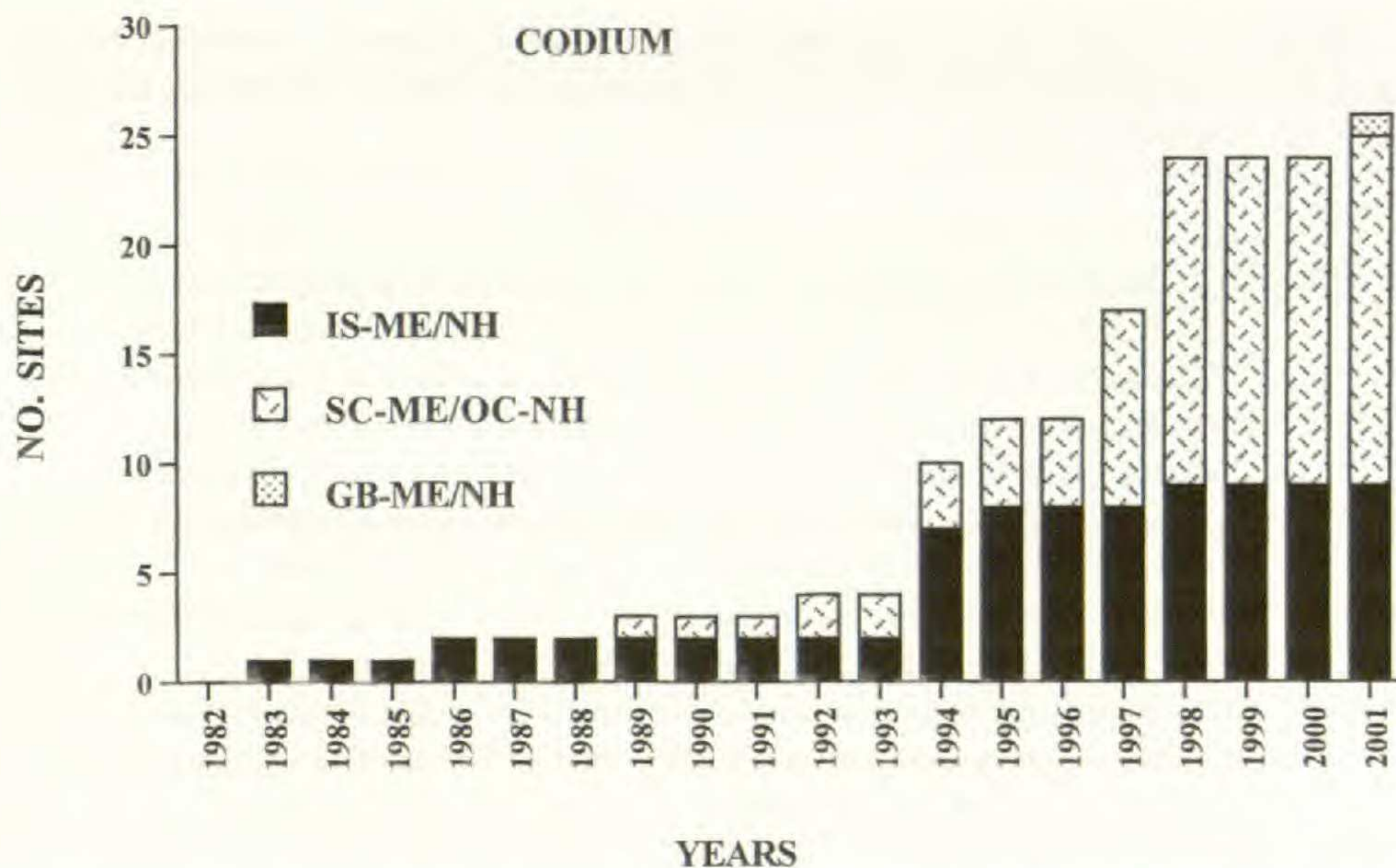


Figure 6. Annual variation of attached *Codium* populations (i.e., number of sites) within southern Maine and New Hampshire between 1982 and 2001, with the data being based upon seasonal collections at 276 open coastal and estuarine locations. Abbreviations: Isles of Shoals = IS-ME/NH; southern ME coast and nearshore NH open coast = SC-ME/OC-NH; Great Bay Estuarine System = GB-ME/NH.

Hampton-Seabrook Estuarine System. The 1985 drift sample from Weeks Point is well beyond its current distribution (Figure 2; Appendix), which is decidedly coastal (82%).

**Variability of subtidal communities at the Isles of Shoals.** Figure 7 shows the relative abundance of four subtidal canopy species at the Isles of Shoals based upon two depth groupings (0 to  $-7$  m and  $-8$  to  $-12$  m) and a composite of five contiguous locations. *Codium* dominates the shallow subtidal zone ( $\sim 77\%$  cover), while the three native taxa are rare at these depths ( $\sim 0.7$ – $1.1\%$  cover). By contrast, the mid-subtidal zone has a mixture of the four species: *Agarum clathratum* ( $\sim 21\%$  cover), *Codium* ( $\sim 29\%$  cover), *Desmarestia aculeata* ( $\sim 16\%$  cover), and *Laminaria* spp. ( $\sim 15\%$  cover). An assessment of percent coverage variability for the different shallow-water populations indicates that they are relatively uniform, with standard deviations only ranging from  $\pm 0.7\%$  (*Desmarestia*) to  $\pm 2.3\%$  (*Codium*). Variability of the four taxa is much greater within the mid-subtidal, ranging from  $\pm 9.7\%$  (*Laminaria* spp.) to  $\pm 28\%$ . Some of



Table 1. Local chronology and dispersal of *Codium* in southern Maine and New Hampshire following its colonization in 1964 at Boothbay Harbor, ME (cf. Figure 1 and 2).

| Year | Localities  |
|------|---|
| 1982 | Drift populations initially found on Appledore Island, Kittery, ME, Isles of Shoals (Dr. A. Borror, emeritus Professor, Dept. Zoology, Univ. New Hampshire, pers. comm.; Prince 1988)   |
| 1983 | First attached populations found at the Isles of Shoals within Babb's Cove on the western (i.e., sheltered) side of Appledore Island, Kittery, ME near the Shoals Marine Laboratory (cf. Carlton and Scanlon 1985 for P. Sze's initial record)  |
| 1984 | Attached populations found at Babb's Cove and contiguous sheltered sites on Appledore Island, Kittery, ME   |
| 1985 | Detached populations recorded from Rye Ledge, Rye, NH (near-shore open coast) and at Weeks Point, NH (inner reaches of the Great Bay Estuary System)  |
| 1986 | Dense subtidal beds (1–13 m below MLW) found at many sheltered Appledore Island, ME sites, particularly where kelps had been stripped by urchin grazing (Prince 1987); attached populations recorded from the Gosport Harbor (i.e., sheltered) side of Smuttynose Island, Kittery, ME   |
| 1988 | Student transect studies documented the presence of <i>Codium</i> (6–12% coverage) in the low intertidal zone at three sheltered transect sites (i.e., T2, T5, and T24) on Appledore Island, Kittery, ME (cf. Table 2)  |
| 1989 | Student transect studies on Appledore Island, Kittery, ME documented the presence of <i>Codium</i> (7% coverage) at a fourth sheltered transect site (i.e., T28; cf. Table 2); first attached populations recorded from the nearshore open coast of southern Maine at Cape Neddick, York  |
| 1992 | Abundant at several sheltered locations on Appledore and Smuttynose Islands, Kittery, ME (i.e., within Gosport Harbor); first record of attached populations from the nearshore open coast of New Hampshire at Fort Stark (Jaffrey Point), Newcastle  |
| 1993 | Well established on the exposed side of Appledore Island, Kittery, ME (L. G. Harris, unpubl. obs.)  |
| 1994 | First attached populations found at Duck and Malaga Islands, Kittery, ME, plus Lunging, Seavey, and White Islands, Rye, NH at the Isles of Shoals; attached populations found at Rye Ledge, Rye, NH on the nearshore open coast, plus drift populations at Long Sands, York, ME and Odiorne Point State Park, Rye, NH                     |
| 1995 | Initial attached populations found on Star Island, Rye, NH; abundant populations also found on the exposed side of Smuttynose Island, Kittery, ME; student transect studies on Appledore Island, ME documented increased coverage (12–15%) on transects T2 and T4 (Table 2); initial attached populations found at Odiorne Point, Rye, NH |



Table 1. Continued.

| Year | Localities   |
|------|--|
| 1997 | Attached populations found at Seapoint, Kittery, ME on the near-shore open coast, at three nearby sites within the outermost part of Brave Boat Harbor Marsh, York-Kittery, ME, and at Great Boar’s Head, Rye, NH  |
| 1998 | Attached populations initially found at Cedar Island Ledge, ME, Isles of Shoals, plus at two other outer Brave Boat Harbor, York-Kittery, ME sites, and nearby Sisters Point and Fort Foster on Gerrish Island, Kittery, ME; initial collections also found at North Wallis Sands and Concord Point, Rye, NH |
| 1999 | Detached populations recorded from the Knowles Island area, Hampton-Seabrook Estuary System, NH  |
| 2001 | Attached population found within South Mill Pond (i.e., backwater of Piscataqua River), Portsmouth, NH and at a site just south of Odiorne Point State Park, Rye, NH   |

this variability is no doubt associated with the historical presence or absence of urchin “barrens,” with White Island, NH always having kelp beds and the others urchin barrens. The consistent shallow-water dominance of *Codium* at the Shoals suggests that it has become “adapted” to diverse exposure conditions. The presence of young plants among established adults also indicates that it will persist for some time.

**Demographic patterns of *Codium* populations at six Gulf of Maine sites.** Figure 8 illustrates the size frequency and mean ( $\pm$  SD) stature (frond length) of *Codium* populations at Jaquish Island, Cape Neddick, Seapoint, and Brave Boat Harbor, ME, plus South Mill Pond and Star Island, NH. The highest frequency (35.4%) of large fronds (41–80 cm long) was recorded at Star Island, while 100% of the plants were small (0–20 cm long) in the relatively deep salt marsh pannes at Brave Boat Harbor ( $\sim 0.6 \pm 0.7$  m,  $n = 21$ ). Mean frond length and frequency patterns corresponded, being highest at Star Island ( $28.5 \pm 17.0$  cm) and lowest at Brave Boat Harbor ( $10.9 \pm 3.2$  cm). Table 3 summarizes the values for mean frond weight, length, density, and biomass, plus the percent occurrence values per site; no weight and biomass values are shown for Cape Neddick (cf. Materials and Methods section). Mean frond weights were smallest at Brave Boat Harbor ( $11.2 \pm 16.6$  g) and largest at Star Island ( $177.4 \pm 198.9$  g). Tide pool populations at Jaquish Island had the highest



Table 2. Percent coverage of *Codium fragile* subsp. *tomentosoides* within the low intertidal zone on four sheltered permanent transects (T2, T5, T24, and T28) at Appledore Island, Maine, Isles of Shoals during 1986–1995. — = no sample taken.

| Transect | % Coverage |      |      |      |      |      |      |      |      |      | Mean $\pm$ SD (SE)     |
|----------|------------|------|------|------|------|------|------|------|------|------|------------------------|
|          | 1986       | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 |                        |
| T2       | 0          | 0    | 6.0  | 2.0  | 4.0  | 0    | 2.0  | 0    | 4.0  | 15.0 | 3.3% $\pm$ 4.6% (1.4%) |
| T5       | 0          | 0    | 8.0  | 3.0  | 16.0 | 0    | 0    | 1.0  | 0    | 0    | 2.8% $\pm$ 5.3% (1.7%) |
| T24      | —          | 0    | 12   | 0    | 4    | 0    | 5    | 0    | 1    | 12   | 3.8% $\pm$ 5.0% (1.7%) |
| T28      | 0          | 0    | 0    | 7    | 0    | 1.0  | 0    | 0    | 0    | 1.0  | 0.9% $\pm$ 2.2% (0.7%) |



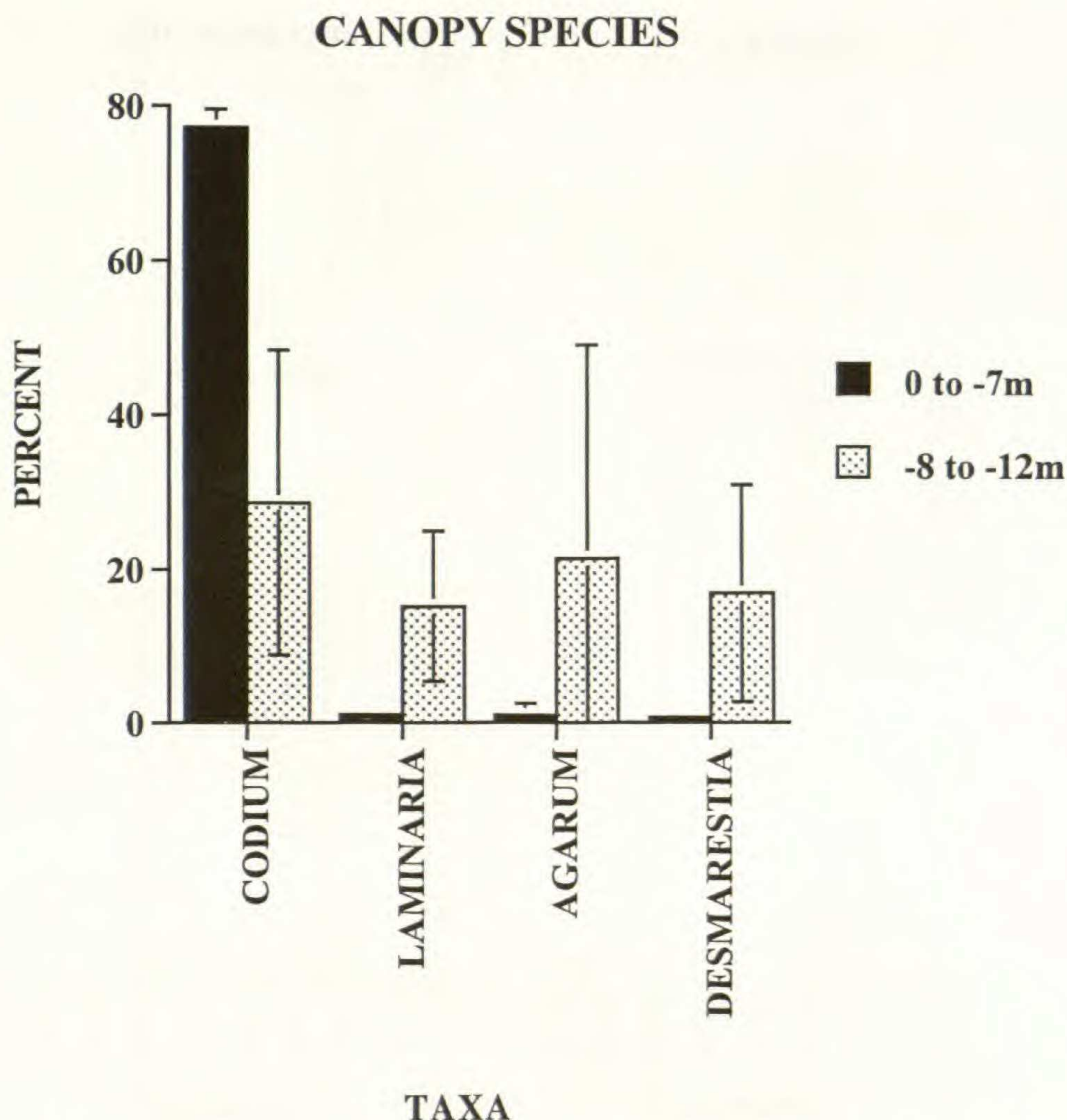


Figure 7. Relative abundance of four subtidal canopy species at the Isles of Shoals, based upon two depth intervals (0 to -7 m and -8 to -12 m) and a composite of five contiguous locations measured in 2000.

density ( $49.0 \pm 79.4$  plants/m<sup>2</sup>) and Cape Neddick the lowest ( $0.1 \pm 0.4$  plants/m<sup>2</sup>). Biomass was greatest at Star Island ( $6103.0 \pm 4137.0$  g/m<sup>2</sup>) and lowest at Brave Boat Harbor ( $4.0 \pm 1.0$  g/m<sup>2</sup>). Linear- and area-based comparisons of density and biomass at Brave Boat Harbor showed dramatic differences, with densities of  $107 \pm 93$  plants/m versus  $0.4 \pm 0.06$  plants/m<sup>2</sup> and biomass values of  $1198.4 \pm 1543.8$  g/m and  $4.0 \pm 1.0$  g/m<sup>2</sup>. Percent occurrence was highest at Star Island (100%) and lowest at Cape Neddick (7.5%).

**Occurrence of encrusting invertebrates and algal epiphytes on *Codium*.** Older, perennial fronds of *Codium* are often heavily



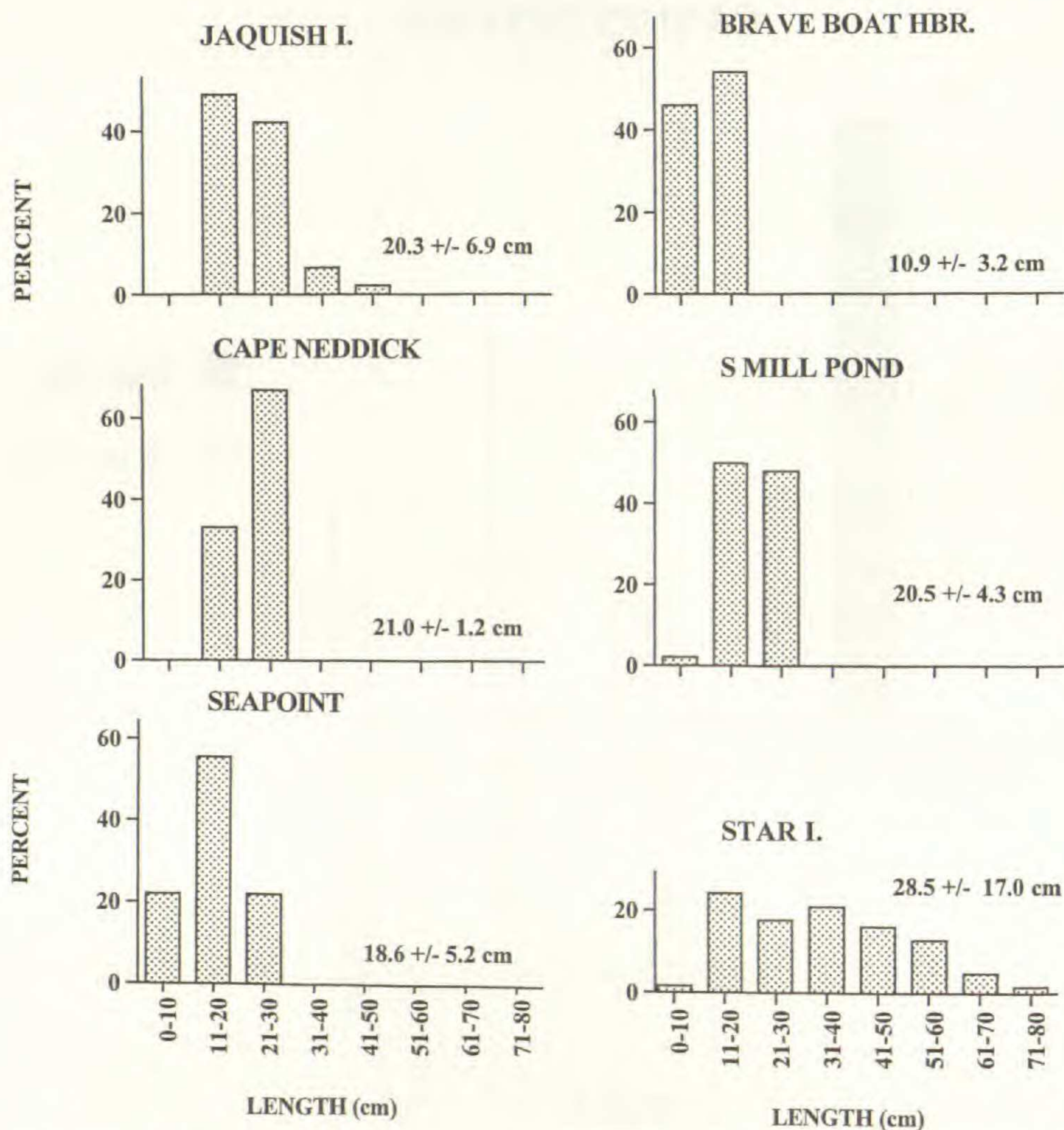


Figure 8. Size frequency distribution patterns for *Codium* frond lengths (cm) at six Gulf of Maine sites, plus mean frond lengths  $\pm$  SD.

overgrown by encrusting, colonial invertebrates and epiphytes, including the introduced bryozoan *Membranipora membranacea* and the non-native tunicates *Botrylloides violaceus* Oka and *Diplosoma listerianum* (Milne-Edwards). Based upon recent sampling (June 21, 2000) of three major subtidal canopy species at Star Island, NH (i.e., *Codium*, *Agarum clathratum*, and *Laminaria saccharina*) it appears that winter survival of *M. membranacea* is higher on *Codium* than kelps, presumably because the blades of *Codium* stay intact while kelps slough off their terminal fronds and associated epibionts (cf. Lambert et al. 1992). Thus, approximately 76% of the *Codium* thalli sampled had abundant *M. mem-*



Table 3. Mean ( $\pm$  SD) frond weight, length, density, biomass, and percent occurrence of *Codium* populations at six sites ranging from mid-coastal Maine to New Hampshire. <sup>a</sup> Units for area-based assessment. <sup>b</sup> Units for linear-based assessment.

| Sites   | Frond Weight<br>(g) | Frond Length<br>(cm) | Density<br>(no./m <sup>2</sup> ) <sup>a</sup><br>or (no./m) <sup>b</sup> | Biomass, Fresh Wt.<br>(g/m <sup>2</sup> ) <sup>a</sup><br>or (g/m) <sup>b</sup> | % Occur-<br>ence |
|---|---------------------|----------------------|--|---|------------------|
| Area-based Assessment                                   |                     |                      |  |   |                  |
| Jaquish Island, Harpswell, ME<br>(nearshore open coast) | 49.5 $\pm$ 58.4     | 20.3 $\pm$ 6.9       | 49.0 $\pm$ 79.4  | 2423.0 $\pm$ 4637.0   | 50.0             |
| Cape Neddick, York, ME<br>(nearshore open coast)        | —                   | 21.0 $\pm$ 1.2       | 0.1 $\pm$ 0.38   | —   | 7.5              |
| Brave Boat Harbor, Kittery, ME<br>(outer estuarine)     | 11.2 $\pm$ 16.6     | 10.9 $\pm$ 3.2       | 0.4 $\pm$ 0.6  | 4.0 $\pm$ 1.0   | 26.3             |
| Seapoint, Kittery, ME<br>(nearshore open coast)         | 18.8 $\pm$ 5.03     | 18.6 $\pm$ 5.2       | 1.4 $\pm$ 1.9  | 26.6 $\pm$ 9.6  | 5.0              |
| South Mill Pond, Portsmouth,<br>NH (outer estuarine)    | —                   | 20.5 $\pm$ 4.3       | 24.0 $\pm$ 33.0  | 3049.6 $\pm$ 4047.2   | 55.5             |
| Star Island, NH, Isles of Shoals<br>(offshore island)   | 177.4 $\pm$ 198.9   | 28.5 $\pm$ 17.0      | 34.4 $\pm$ 20.8  | 6103.0 $\pm$ 4137.0   | 100              |
| Linear-based Assessment                                 |                     |                      |  |   |                  |
| Brave Boat Harbor, Kittery, ME<br>(outer estuarine)     | —                   | —                    | 107.0 $\pm$ 93.0   | 1198.4 $\pm$ 1543.8   | —                |



Table 4. Percent occurrence of different epiphytes on *Codium* samples collected throughout the Gulf of Maine (cf. Appendix).

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**Chlorophyceae**

- Chaetomorpha linum* (O. F. Müll.) Kütz. (entangled, 0.7%)  
*Chaetomorpha picquotiana* Mont. ex Kütz. (entangled, 0.7%)  
*Cladophora sericea* (Huds.) Kütz. (0.7%)  
*Spongomorpha spinescens* Kütz. (0.7%)  
*Ulva lactuca* L. (1.3%)

**Phaeophyceae**

- Ectocarpus fasciculatus* Harv. (0.7%)  
*Melanosiphon intestinalis* (D. A. Saunders) M. J. Wynne (0.7%)  
*Petalonia fascia* (O. F. Müll.) Kuntze (0.7%)  
*Pilayella littoralis* (L.) Kjellm. (0.7%)  
*Sphacelaria cirrosa* (Roth) C. Agardh (3.3%)

**Rhodophyceae**

- Callithamnion tetragonum* (With.) S. F. Gray (0.7%)  
*Ceramium virgatum* Roth (5.3%)  
*Ceramium strictum* Harv. (0.7%)  
*Cystoclonium purpureum* (Huds.) Batters (0.7%)  
*Erythrotrichia carnea* (Dillwyn) J. Agardh (0.7%)  
*Neosiphonia harveyi* (Bailey) Kim, Choi, Guiry & G. W. Saunders (23.3%)  
*Palmaria palmata* (L.) Kuntze (0.7%)  
*Polysiphonia fucoides* (Huds.) Grev. (0.7%)  
*Spermothamnion repens* (Dillwyn) Rosenv. (2.0%)  
*Titanoderma pustulatum* (J. V. Lamour.) Nägeli (0.7%)  
 "Trailliella intricata" stage of *Bonnemaisonia hamifera* Har. (0.7%)

**Cyanophyceae**

- Microcoleus lyngbyaceus* (Kütz.) P. Crouan & H. Crouan (0.7%)

**Bacillariophyceae**

- Berkeleya rutilans* (Trentophohl) Grünow (3.3%)
- 

*branacea* on their midportions and often on multiple blades, while most kelps only had small residual colonies near their tips. Of the two kelps, *L. saccharina* exhibited a lower frequency of *M. membranacea* (~7.0%) than *A. clathratum* (~69%). In assessing 150 samples of *Codium* throughout the Gulf of Maine (Appendix), 21 algal epiphytes were recorded, including one macroscopic benthic colonial diatom, 3 green, 5 brown, 11 red algae, and 1 cyanobacteria (Table 4). Two filamentous green algae, *Chaetomorpha linum* (O. F. Müll.) Kuntze and *C. picquotiana* Mont. ex Kütz., were occasionally found entangled amongst



*Codium*. The relative abundances of the different epiphyte taxa are also summarized in Table 4, with the Asiatic red alga *Neosiphonia harveyi* being most conspicuous (23.3% occurrence), followed by five native species: *Ceramium virgatum* Roth [= *C. rubrum* (Huds.) Batters; cf. Maggs et al. 2002 (5.3%)]; *Sphacelaria cirrosa* (Roth) C. Agardh (3.3%), *Berkeleya rutilans* (Trentopohl) Grönöw (3.3%), *Spermothamnion repens* (Dillwyn) Rosenv. (2.0%), and *Ulva lactuca* L. (1.3%). The other 15 epiphytic taxa were restricted to a single site (0.07%), while the two entangled *Chaetomorpha* species exhibited a similar pattern. Although *Codium* typically grows on hard substrata (i.e., rocks and/or shellfish), one epiphytic population was found on *Ascophyllum nodosum* (L.) Le Jol. and another on *Fucus vesiculosus* L. var. *sphaerocarpus* J. Agardh. The spatial distribution of diverse epiphyte populations within the Gulf of Maine is shown in Figure 4B, expressed as the number of site records (cf. Appendix) within each of the 12 contiguous habitats described above. The dominance of red algae, particularly *N. harveyi*, is readily apparent, plus a major peak within Maine's "Indented Coastline."

#### DISCUSSION

It should be emphasized that the invasion of the Gulf of Maine by *Codium* occurred at two locations and times: (1) mid-coastal ME near Boothbay Harbor in 1964, probably via transplantation of oysters from Long Island (i.e., *Crassostrea virginica* Gmel. and/or *Ostrea edulis*) with small microscopic plants (Boerner 1972; Coffin and Stickney 1966; Davis 1971; Malinowski 1974); and (2) southern MA due to the expansion of attached plants from the Cape Cod Canal (1969) into nearby Cape Cod Bay during 1972 (Carlton and Scanlon 1985; Coleman and Mathieson 1974; Fairbanks et al. 1971). The prevalence of populations downstream from the initial Boothbay Harbor site (Figure 4A) suggests that the first attached plants (Figure 5A–5D) grew, fragmented (Figure 5E–5H), and were then carried southward by strong currents (A. Borror, pers. comm.; Brooks 1985; Harris and Mathieson 2000; Prince 1988). The limited occurrence of contiguous populations just north of Boothbay at Bristol and South Bristol, ME suggests that dispersal of its single-celled reproductive cells ("gametes") is restricted by south-flowing currents (Apollonio 1979; Bigelow 1927; Mathieson et al. 1991). The second more southerly pattern



suggests an expansion of attached plants after their passage through the Cape Cod Canal (1969–1972), which connects Buzzards and Cape Cod Bays (Carlton and Scanlon 1985; Coleman and Mathieson 1974).

Because of the warm-water affinities of *Codium* (Fralick and Mathieson 1973; Lüning 1990), it initially expanded more rapidly south than north of Cape Cod, dominating shallow subtidal habitats. By contrast, populations in Boothbay Harbor were initially (1964 to the early 1970s) “quiescent,” long-lived, and rather circumscribed (Coffin and Stickney 1966; Fralick 1970; Fralick and Mathieson 1973); ultimately, their biomass and stature increased, allowing a drifting of detached fragments like those first observed at the Shoals in 1982 (Table 1; i.e., ~125 km SW of Boothbay Harbor, ME). According to Searles et al. (1984) it took nine years for the first significant southward expansion of *Codium* from eastern Long Island (1957) to Barnegat Bay, New Jersey (Taylor 1967); 10 years later Hillson (1976) discovered a population in Virginia, 250 km south of New Jersey; in 1979 it was collected near Cape Hatteras, North Carolina, with this representing another 450 km southern extension (Searles et al. 1984). Once established in North Carolina it has spread rapidly throughout several inlets and sounds between Cape Fear and Cape Lookout, south of Cape Hatteras. Thus, it took variable and often extensive time periods (i.e., decades) for such expansions (Burrows 1991; Carlton and Scanlon 1985). The rate of spread described above is comparable to that noted from Boothbay Harbor, ME (1964) to the NH/ME Isles of Shoals (1983), and the nearshore open coast of southern ME (1989) and NH (1992). According to Hubbard and Garbary (2001, 2002) the distribution and spread of *Codium* within eastern Canada has also been very rapid; that is, within 10 years of its discovery on the south shore of Nova Scotia (Bird et al. 1993) it has dispersed over 1200 km to sites in northern Nova Scotia, New Brunswick, and Prince Edward Island. Hubbard and Garbary (2001, 2002) also note that two groups of plants seem to occur, with one being smaller, regularly dichotomously branched, and having flat-topped utricles with small mucrons [i.e., like *C. fragile* subsp. *atlanticum* (Cotton) P. C. Silva] and the other larger, more irregularly branched and having utricles with lanceolate tips and larger mucrons (i.e., *C. fragile* subsp. *tomentosoides*). Whether these different morphologies represent independent introductions, adaptations to local environments, or patterns of phenotypic plas-



ticity needs to be established (cf. Garbary and Jess 2000; Hubbard and Garbary 2002).

The growth of *Codium* in the Gulf of Maine varies seasonally and spatially, being greatest during peak summer temperatures and insolation. Elongation rates of  $\sim 5.5$  and  $\sim 10$  cm/month have been recorded at Boothbay Harbor, ME and southern MA, respectively (Fralick and Mathieson 1973) versus 2.7–8.4 cm/month in Rhode Island (Hanisak 1979a). Like many other warm-temperate organisms found north of Cape Cod, MA (Hooper et al. 2002; Mathieson and Hehre 1986), *Codium* is most abundant at scattered warm water sites like Boothbay and Brave Boat Harbors, ME, the Isles of Shoals, NH/ME (Figure 3), and inner South Mill Pond, NH (Carlton and Scanlon 1985; Harris and Mathieson 2000; Loder et al. 1983; Mathieson et al. 2001; C. C. Taylor et al. 1957), with its growth (and reproduction) probably restricted by winter cold-water temperatures (Hutchins 1947). After its initial expansion into Cape Cod Bay, MA (1969), *Codium* demonstrated its warm-water affinities as it was reported (1974) at the nuclear power station at Plymouth, MA within Cape Cod Bay shortly after it commenced operation and warm-water discharge (Carlton and Scanlon 1985). In discussing the introduction of *Codium* into the southern Gulf of St. Lawrence, Garbary et al. (1997) speculated that many of the negative features associated with its presence on Cape Cod, namely its adverse effects on shellfish and the fouling of tourist beaches (Hanisak 1980; Sheran and Prince 1973), may ultimately occur within the southern Gulf of St. Lawrence because of similarities of subtidal habitats.

The growth of *Codium* is initiated at 10–12°C; it is optimal at  $\sim 21$ –24°C, and it can survive  $-2.0^\circ\text{C}$  (Fralick and Mathieson 1973; Hanisak 1979a, 1980; Malinowski and Ramus 1973; Moeller 1969). At some shallow-water locations, *Codium* becomes fragmented during winter, leaving only a residual basal holdfast from which it may regenerate (Fralick and Mathieson 1972; Hanisak 1980). At other (i.e., deeper) subtidal locations, such as Cape Neddick, York, ME and the NH/ME Isles of Shoals, plants may be “quiescent” or cease growth during winter, but they continue to increase in stature for two or more years (Harris and Mathieson 2000; Harris and Tyrrell 2001). Malinowski and Ramus (1973) studied the growth of *Codium* in the Niantic River Estuary of Connecticut, finding that it was initiated when temperatures and salinities exceeded 10°C and 22‰, respectively and



was greatest at  $> 16^{\circ}\text{C}$  and  $> 27\text{‰}$ . According to Hanisak (1979a, 1980), the light-physiology of *Codium* is of critical importance in determining its seasonal growth and competition with other seaweeds. It exhibits a low light saturation requirement, yet is efficient under higher light levels. He stated that limited nitrogen availability during summer limits its growth (cf. Hanisak 1979b, 2001). Even so, *Codium* is quite competitive in obtaining nitrogen during periods of low nutrient availability, and it can grow equally well on nitrate, nitrite, ammonium, and urea. It can take up different forms of inorganic nitrogen simultaneously and at relatively high rates, providing a major competitive advantage. Although *Codium* does not grow appreciably during winter, it is capable of taking up nitrogen and storing it until spring growth.

Reproduction in *Codium fragile* subsp. *tomentosoides* occurs either by motile unicells or vegetative fragments (Boerner 1972; Churchill and Moeller 1972; Fralick and Mathieson 1972; Garbary et al. 1997; Malinowski 1974; Malinowski and Ramus 1973; Moeller 1969; Ramus 1971, 1972; Rosenvinge 1920). Initiation of motile unicells, which have been variously designated as gametes or zoospores, occurs between  $12\text{--}15^{\circ}\text{C}$  (Churchill and Moeller 1972), and it is maximal at  $\sim 24^{\circ}\text{C}$  (Hanisak 1979a). In the North Pacific, biflagellate anisogamous gametes have been reported, resulting in zygotes, initial dissociated filaments, and ultimately erect thalli (Arasaki et al. 1955; Borden and Stein 1969; Williams 1925). By contrast, most accounts of North Atlantic populations have reported either no male gametangia (Garbary et al. 1997; Ramus 1972) or parthenogenetic female gametes (Churchill and Moeller 1972; Fralick and Mathieson 1973; Hanisak 1979a; Lüning 1990; Moeller 1969); again the latter cells initially produce a juvenile tuft of dissociated filaments from which erect thalli grow under favorable conditions (Fletcher et al. 1989; Ramus 1972; Yang et al. 1997). Similar patterns of parthenogenetic female gametes have been reported from the Atlantic and Mediterranean coasts of France (Dangeard 1958; Dangeard and Parriaud 1956; Delépine 1959; Feldmann 1956; Parriaud 1957). Prince (1988) and Prince and LeBlanc (1997) found both large and small cells within the same gametangia for Appledore, ME populations of *Codium*, with the larger ones (female) being approximately six times more numerous than the smaller ones (male). Fusion appears to require gametes from different gametangia if not from different plants. They stated that this was the



first report of *Codium* producing male and female gametes within the same gametangium (Arasaki et al. 1955; Borden and Stein 1969; Williams 1925), which is unique for algae in general (Burr and West 1970; Feldmann 1956). Churchill and Moeller (1972) found variable-sized swarmers in the same gametangia of Long Island populations; however, there was no sign of fusion nor did they differentiate male and female gametes. Several other investigators have reported variable-sized swarmers in *C. fragile* subsp. *tomentosoides* (Dangeard 1958; Delépine 1959; Moeller 1969; Weber 1969). In studying five populations of *Codium* ranging from Boothbay Harbor, ME to Long Island Sound, Prince (1990) found male and female gametes in each, the latter always occurring in greater numbers than the former. Surprisingly, two samples from Boothbay Harbor had small cells similar to those described by Coffin and Stickney (1966) and Malinowski (1974).

Several investigators have shown that *Codium* can exhibit extensive vegetative reproduction (Boerner 1972; Chapman 1999; Churchill and Moeller 1972; Fletcher et al. 1989; Fralick and Mathieson 1972; Hanisak 1980; Malinowski 1974; Malinowski and Ramus 1973; Moeller 1969; Ramus 1972; Rosenvinge 1920; Yang et al. 1997). Fletcher et al. (1989) stated that dissociated, siphonaceous filaments (see above) could occur as an independent, widely distributed, and more tolerant stage than the mature, macroscopic growth form; these filaments can propagate themselves vegetatively after detachment, dispersal, and entrapment (cf. Ramus 1972; Yang et al. 1997). Fralick (1970) found that macroscopic fragments were capable of reattachment to any solid substrata after initiating colorless filaments from their terminus (Dromgoole 1975, 1979; Garbary et al. 1997; Hanisak 1979a; Moeller 1969). Chapman (1999) stated that budding of adult thalli may occur during summer, allowing a subsequent release of vegetative juveniles (i.e., fragments) several cm in length. Extensive fragmentation of some shallow-water populations may occur during winter (Fralick and Mathieson 1972; Hanisak 1980; Malinowski and Ramus 1973) because of low temperatures ( $< 9^{\circ}\text{C}$ ) causing thallar constriction, segmentation (Figure 5G), and the production of a pseudoperennial residual base that can produce new fronds the following spring (Dromgoole 1975, 1979; Knight and Parke 1931; Mathieson and Hehre 1986; Sears and Wilce 1975; Trowbridge 1996). Other (i.e., deeper) populations tend to act as true perennials, with their thalli staying intact and often surviving



for several years. Harris and Mathieson (2000) noted that the saccoglossan *Placida dendritica* (Alder & Hancock) had become an important specialized herbivore on *Codium* (cf. Trowbridge and Todd 1999, 2001), causing a reduction of this alga in protected areas (e.g., Gosport Harbor, Isles of Shoals) and facilitating its dispersal by enhanced fragmentation. *Placida* is common in salt marsh environments where it primarily feeds on the siphonaceous green alga *Bryopsis plumosa* (Huds.) C. Agardh, a close relative of *Codium* (Bleakney 1996). The slug aggregates at the junction of shaded, inner branches of *Codium*, puncturing cell walls and pumping out its cytoplasm (cf. Trowbridge 1992). The resulting plants become chlorotic, ragged, and break easily, detaching fragments that may either accumulate within localized (i.e., sheltered) depressions or float away. As outlined above, macroscopic fragments can be produced in many ways; whatever their source they are often quite buoyant (i.e., due to their internal gas entrapment) and very proliferous (Figure 5H), like many detached marsh fucoids (Mathieson and Dawes 2001). These fragments, as well as rafted *Codium* plants on shells, pebbles, and stones, are capable of floating long distances via surficial wind and currents; they may also move on the bottom as deep-drift specimens transported by bottom currents (Anonymous 1967; Bouck and Morgan 1957; Carlton and Scanlon 1985; Churchill and Moeller 1972; Dromgoole 1982; Dromgoole and Foster 1983; Fralick 1970; Galstoff 1962a,b; Garbary et al. 1997; Hanisak 1980; Malinowski 1974; Moeller 1969; Norton and Mathieson 1983; Parkes 1975; Ramus 1971; Rosenvinge 1920; Taylor 1967). The magnitude of this drifting process is suggested by the extensive accumulation of rafted *Codium* populations on Cape Cod and other Atlantic beaches (Ben-Avraham 1971; Carlton and Scanlon 1985; Grieve 1929).

Fralick (1970) suggested that *Codium* could be dispersed on migrating molluscs, as mature plants have been collected on oyster shells off the Delaware coast at depths of 200 feet (Anonymous 1967). He further speculated that it may be dispersed by herbivorous invertebrates, such as the green urchin *Strongylocentrotus droebachiensis*, which can contain healthy-looking reproductive structures (gametangia) in its fecal material. Although it is not a preferred food source, some shallow-water molluscs may graze upon *Codium* (Prince and LeBlanc 1992; Trowbridge 1995). Carlton and Scanlon (1985) stated that it has probably



been spread most extensively by humans via ships' hulls, ballast water, fishing nets, aquaculture projects, etc. Loosanoff's (1955) early transplant experiments with the European oyster *Ostrea edulis* should be noted, as he transferred ~3000 oysters from Holland to Boothbay Harbor, ME during late 1949 or early 1950. His experiments were successful but he warned against the impending danger of such transplants!

Many of the invasive traits of *Codium* parallel those of the introduced tropical/subtropical green alga *Caulerpa taxifolia* within the Mediterranean (Boudouresque et al. 1994; Meinesz 1999; Meinesz et al. 1993; Raloff 1998; Trowbridge 1998; Wiedenmann et al. 2001) and recently reported from California (Jousson et al. 2000). It is taller than native populations, grows more vigorously, is more tolerant to cold temperatures, and capable of reproducing itself asexually via fragmentation (cf. Aleem 1992; Modena et al. 2000). Raloff (1998) suggested that the Mediterranean plant may be a hybrid or a new species that evolved through selective pressure in the aquarium industry. Prince (1988) stated that Appledore, ME populations of *Codium* may represent a new ecotype because of its unusual mode of reproduction (i.e., anisogametes in the same gametangia) and the fact that it has spread rapidly at water temperatures between 0–18°C (Loder et al. 1983), previously thought to be unsuitable for this species (Fralick and Mathieson 1973). Malinowski (1974) suggested that Boothbay Harbor populations may have diverged through natural selection from southern ones, as their germlings are able to grow at 4°C, while those from “parental” Long Island Sound cannot. He noted that Boothbay Harbor plants grew significantly less at higher temperatures (18–24°C) than did other populations. Krapraun and Martin's (1987) cytological studies of North Carolina *C. fragile* subsp. *tomentosoides* suggest that nuclear variability might have occurred, as the plant's haploid chromosomes were enlarged and exhibited increased DNA content versus autochthonous species. Such cytological patterns parallel the well-known polyploid features of other weedy species (Lüning 1990). Using DNA restriction studies, Goff et al. (1992) found that North Atlantic populations of the adventive subsp. *tomentosoides* differed from the closely related Northeast Pacific subsp. *fragile*. The subsp. *novae-zealandia* on New Zealand shores also differed physiologically from subsp. *tomentosoides* (Dromgoole 1980, 1982; Dromgoole et al. 1979).



As noted by Trowbridge (1995), the density of *Codium* varies geographically, with 10,170 thalli/m<sup>2</sup> being recorded near Cape Cod, MA (Fralick and Mathieson 1973), ~20 adult thalli/m<sup>2</sup> in Connecticut (Malinowski 1974), and 12–84 thalli/m<sup>2</sup> in Rhode Island (Hanisak 1979a). Typically, densities of *Codium* in New Zealand (Dromgoole 1979) were lower than those reported for southern New England, while they were more comparable to Gulf of Maine populations (Table 3). Trowbridge (1995) suggested several potential reasons for this differential: (1) the population size of New Zealand plants is still increasing, while reports from the North Atlantic indicate that it takes several decades to reach high densities (Burrows 1991; Carlton and Scanlon 1985; Table 3); (2) the New Zealand species-rich communities may be more resistant to invasion than species-poor communities like the northwestern Atlantic (Chapman 1999; Chapman et al. 2001, in press; Diamond and Case 1986; Elton 1958); (3) the presence of indigenous species that are ecologically and/or taxonomically similar may contribute to biotic or community resistance (Baltz and Moyle 1993; Diamond and Case 1986; Moulton and Pimm 1984); (4) the New Zealand populations studied by Dromgoole (1979) were mostly intertidal while those in southern New England were primarily subtidal; (5) salinity patterns in the two areas differed, the Hauraki Gulf of New Zealand being fully marine (~35‰) and the northwestern Atlantic less saline (32‰); and (6) the annual variability of surface water temperatures in the Hauraki Gulf is more limited (~12–21°C) than the northwestern Atlantic where winter conditions are much cooler (0°C). Harris and Mathieson (2000) documented differential density patterns for *Codium* at the Shoals, with the species initially being most abundant and dense in sheltered areas (1984–1990) and subsequently (1991) expanding to more exposed sites (cf. Table 1). Although the mechanism by which this shift in habitat breadth occurred is unknown, it may have been associated with extensive overgrowth of *Laminaria* spp. by the introduced bryozoan *Membranipora membranacea*, facilitating expansion of *Codium*. Harris and Tyrrell (2001) emphasized that *Codium* was not the only species undergoing a rapid expansion at this time.

Most *Codium* populations from nearshore open coastal sites in southern Maine and New Hampshire are smaller and have more limited densities and biomass than at warmer offshore insular sites like Star Island, NH (cf. Figures 3, 8; Table 3). For example,



only small aggregations were present at Seapoint, ME; further they were smaller in stature (mean = 18.6 cm, 18.8 g), slightly branched, and had limited densities (1.4 plants/m<sup>2</sup>) and biomass (mean = 27.0 g/m<sup>2</sup>). By contrast, at protected Star Island sites the stature of *Codium* was larger (mean = 28.5 cm, 177.4 g), it was extensively branched, and it had high densities (mean = 34.4 plants/m<sup>2</sup>) and biomass values (mean = 6103.0 g/m<sup>2</sup>). Early studies (1964–1965) by Coffin and Stickney (1966) at Boothbay Harbor, ME showed a dominance of relatively small plants throughout the year (mean = 10.5–23.0 cm) and modest winter growth rates of ~5 cm/month. Fralick (1970) compared the stature and biomass of *Codium* populations at a southern New England site near Wings Neck, Bourne, MA (41°31'N, 70°40'W), finding the plants to be relatively small (rarely exceeding 30 cm) and exhibiting a seasonal biomass variation of ~350 g/m<sup>2</sup> (February) to ~2900 g/m<sup>2</sup> (August). Thus, its stature was similar to nearshore populations in mid-coastal Maine and New Hampshire, while its peak summer biomass was approximately half (48%) that recorded at Star Island and much higher (197–725×) than those at other nearshore sites. The stature and biomass of Star Island populations suggest a more optimal temperature regime (Figure 3) and a relatively mature community versus nearshore populations in mid-coastal Maine and New Hampshire (Table 3). In characterizing Nova Scotian populations of *Codium*, Bird et al. (1993) noted that they were relatively large (50–60 cm maximum) and abundant subtidally (i.e., like those at Star Island).

The contrasting patterns of insular versus nearshore populations described above may be associated with enhanced temperature stratification at the former (Figure 3) versus the latter habitats (cf. Lambert and Harris 2000; Loder et al. 1983). That is, offshore winds appear to cause nearshore upwelling and lower temperatures that reduce the growth and reproductive potential of these populations (see above). Harris et al. (1996) also described a pattern of increasing summer temperatures within the southern Gulf of Maine, which enhanced the growth of *Codium* and altered its community interactions at the Isles of Shoals (Figure 7). For example, it now dominates a variety of shallow (i.e., warmer) subtidal habitats above the thermocline (~–10 m), with *Agarum clathratum* and *Laminaria* spp. occurring below (Harris and Mathieson 2000). During the 1970s and 1980s both kelps were spatially separated, with *Laminaria* occurring above and *Agarum* be-



low the  $\sim -10$  m thermocline (Hulbert 1980; Martin et al. 1988; Tacy et al. 1977; Witman 1984, 1985, 1987; Witman et al. 1982). Thus, changing environmental conditions and community instability due to overfishing of urchins and multiple introductions may have provided an ecological vacuum that *Codium* could fill, expanding its abundance and distribution (Chapman et al. 2001; Harris and Tyrrell 2001; Hay 1990; Malinowski and Ramus 1973; Prince 1989; Prince and LeBlanc 1992; Sanderson 1990; Scheibling 2001; Trowbridge 1995). Garbary et al. (1997) described an analogous pattern within the Gulf of St. Lawrence (Nova Scotia) where *Codium* grows in scours of eelgrass beds (i.e., *Zostera marina* L.) caused by storms or ice damage.

The rapid spread of the red alga *Neosiphonia harveyi* throughout the northwestern Atlantic suggests a variety of interesting parallels with *Codium*, as both species are invasive warm-temperate Asiatic species. The status of *N. harveyi* as a non-indigenous taxon has just recently been clarified (McIvor et al. 2000, 2001) based upon detailed molecular studies (cf. Rueness and Rueness 2000). Its abundance, along with several other epiphytes (Table 4), suggests that *Codium* beds may enhance their development and potential transport via drifting fragments (cf. Bartsch and Kuhlenskamp 2000). The enhancement of epiphyte populations on older perennial plants of *Codium* contrasts with the intercalary growth and sloughing of epiphytes in kelps (Lambert et al. 1992). Epibiontic drag and dislodgement may also be significant factors affecting the dispersal of *Codium* and its associated biota (cf. Witman 1987; Witman and Suchanek 1984). Chapman (1999) stated that the recent establishment and enhancement of the non-native bryozoan *Membranipora membranacea* on kelps within the northwestern Atlantic (cf. Scheibling 2001) may have been facilitated by previous species invasions, allowing an expansion of *Codium* as in the shallow subtidal zone at the Isles of Shoals (Figure 7). That is, *Membranipora* infests and rapidly overgrows large portions of kelp blades, increasing fragility and blade loss, and causing plant loss (Chapman et al. 2001; Chavanich and Harris 2000; Harris and Mathieson 2000; Harris and Tyrrell 2001; Lambert et al. 1992). Until recently *Codium* seems to have been less fouled by *Membranipora* than kelps, allowing a competitive advantage. The bryozoan's potential switching from kelps to *Desmarestia aculeata*, and various red and green algae,



including *Codium* (see above), could provide other competitive interactions.

In summary, the rapid expansion of *Codium* north of Cape Cod, MA shows no sign of decline. Gulf of Maine populations may soon be augmented by Canadian Maritime specimens, which are now abundant and rapidly expanding (Hubbard and Garbary 2001, 2002; Scheibling 2001). Hence, the absence of attached populations within the “Downeast” and Penobscot Bay areas of ME (Figure 4A) may be short-lived, with a future expansion of drifting, south-flowing populations occurring like those described above for mid-coastal ME and other areas of the Atlantic seaboard (i.e., New York to North Carolina). The invasive pattern of *C. fragile* subsp. *tomentosoides* is no doubt based upon its genetic makeup, which is expressed as broad physiological tolerances, extensive vegetative reproduction, morphological plasticity, etc. (Chapman 1999; Dromgoole 1975, 1979; Hanisak 1980). Several weedy life history characteristics are also important, including rapid growth, parthenogenetic development in many populations, dispersal by drifting, etc. (Carlton and Scanlon 1985; Fralick and Mathieson 1972, 1973; Garbary et al. 1997; Hanisak 1979a, 1980; Prince 1988; Trowbridge 1995, 1996). With the exception of a few ascoglossan sea slugs that can cause thallus fragmentation after grazing (Clark 1975; Clark and Franz 1969; Harris and Mathieson 2000; Trowbridge 1993, 1995), *Codium* has largely escaped herbivory within the northwestern Atlantic (Hanisak 1980; Malinowski and Ramus 1973; Ramus 1971; Scheibling 2001, pers. comm.; Trowbridge 1995). The green urchin *Strongylocentrotus droebachiensis* has a low attraction to *Codium*, even though it is capable of consuming it (Freeman and Smith 2000; Prince and LeBlanc 1992). Thus, the lack of a major subtidal herbivore, coupled with the species high potential for dispersal, regeneration, and rapid growth may have allowed it to dominate native species within the Gulf of Maine (Prince 1988; Staehr et al. 2000) and the Canadian Maritime Provinces (Bird et al. 1993; Garbary et al. 1997; Scheibling 2001). In comparing *Codium* abundance in Japan (i.e., original source area), New Zealand, and the northwestern Atlantic, Trowbridge (1995) speculated that it was most abundant in the northwestern Atlantic possibly because low herbivory had allowed its successful invasion (cf. Chapman 1999; Chapman et al. 2001). By contrast, in areas with large endemic grazers, such as the North Pacific where the red



sea urchin *S. franciscana* (A. Agassiz) occurs, *C. fragile* (non-invasive subspecies) is more circumscribed and largely confined to the intertidal (Freeman and Smith 2000). The same authors also noted that the future success of *C. fragile* subsp. *tomentosoides* in areas of differing endemic urchin grazers (e.g., Atlantic, eastern Pacific, New Zealand, Australia) may be influenced by a general decrease in urchin sizes due to local urchin fisheries.

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## APPENDIX

HERBARIUM VOUCHER RECORDS FOR GULF OF  
MAINE *CODIUM* POPULATIONS

## MAINE

WASHINGTON CO: Pembroke, Wilbur's Neck, 8 Oct 1995, *True & Carpenter* (NHA # 63966), = small detached fragments.



LINCOLN CO: Bristol, Rachel Carson Salt Pond Preserve, 20 Oct 1995, *Mathieson* (NHA # 59553), with epiphytic *Neosiphonia harveyi*; South Bristol, tip of peninsula opposite Crow Island and at the end of Rt. 219, 15 Jun 1994, *Hehre, Mathieson & Gerweck* (NHA # 50692, 50771), = drift specimens; 3 Aug 1997, *Mathieson & Dawes* (NHA # 65814, 65815), = attached material with epiphytic *N. harveyi*; South Bristol, Foster's Point, 12 Jul 1995, *Mathieson & Gerweck* (NHA # 58001), with epiphytic *N. harveyi* & *Palmaria palmata*; Southport, Capitol Island, bridge from Cross Road and West Southport, 20 Nov 1995, *Mathieson* (NHA # 60301); Boothbay Harbor, Jul 1964, *Coffin* (MICH # 33991); 26 Sep 1967, *Coffin* (MICH # 33990); Boothbay Harbor, Townsend Gut, 18 Aug 1983, *Morse* (NHA # 48275), collected while harvesting fucoid algae; Boothbay Harbor, Spruce Point, Linekin Neck, 20 Nov 1995, *Mathieson* (NHA # 60371), with epiphytic *N. harveyi*; (NHA # 60372); Boothbay, Ocean Harbor, 14 Mar 2000, *Mathieson* (NHA # 71719), epiphytic on *Ascophyllum nodosum*; Boothbay, East Boothbay Pond, 9 May 1995, *Gerweck* (NHA # 56189), with epiphytic *N. harveyi*; (NHA # 56190); Boothbay, Ocean Point, Linekin Neck, 7 Sep 1994, *Mathieson & Hehre* (NHA # 52461–52462), with epiphytic *Ceramium virgatum*; (NHA # 52463), attached in low tide pool; 29 Sep 1995, *Mathieson* (NHA # 59612), with epiphytic *N. harveyi*.

SAGadahoc CO: Georgetown, Reid State Park, 30 Jun 1994, *Mathieson & Hehre* (NHA # 50653, 52141); 27 Oct 1995, *Mathieson* (NHA # 60209–60210), with epiphytic *Neosiphonia harveyi*; Phippsburg, Head Beach (Casco Bay), 10 Jun 1995, *Mathieson* (NHA # 57830); Phippsburg, Bald Head (Casco Bay), 10 Jun 1995, *Mathieson* (NHA # 58289); 28 Aug 1995, *Mathieson & Hehre* (NHA # 59241–59242), with epiphytic *N. harveyi*; Phippsburg, Sebasco Harbor boat ramp off Rt. 127 (Casco Bay), 9 Sep 1995, *Mathieson* (NHA # 59347), with epiphytic *N. harveyi*.

CUMBERLAND CO: Brunswick, Bunganuc Rock, off Bunganuc Point, Maquoit Bay (Casco Bay), 6 Jun 2001, *Short* (NHA # 74344–74345), growing on rope for a marker buoy; Wharton Point, Maquoit Bay (Casco Bay), 13 Jun 1995, *Mathieson & Hehre* (NHA # 56984); 4 Dec 1995, *Mathieson* (NHA # 59907); Brunswick, Middle Bay Cove, opposite Pennellville, 20 Nov 1999, *Mathieson* (NHA # 70141); Brunswick, Middle Bay, off Pennellville Rd., 20 Nov 1999, *Mathieson* (NHA # 70038, 70209); Brunswick, Mere Point, end of Mere Point Rd., Mere Point Neck, 20 Nov 1999, *Mathieson* (NHA # 70058); 11 Nov 2000, *Mathieson* (NHA # 72964), with epiphytic *Ceramium virgatum* & *Neosiphonia harveyi*; (NHA # 72978), with *Callithamnion tetragonum* & *N. harveyi*; Harpswell, Bailey's Island, end of Rt. 24 near Land's End Store and opposite Jaquish Island (Casco Bay), 6 Sep 1994, *Mathieson & Hehre* (NHA # 53943); Harpswell, Bailey's Island, "the Steps" (Casco Bay), 7 Sep 1999, *Mathieson & Dawes* (NHA # 70191); Harpswell, Jaquish Island (Casco Bay), 6 Jul 2000, *Dawes & Lamson* (NHA # 71749–71753), with epiphytic *N. harveyi*; Harpswell, Lookout Point boat ramp, Middle Bay (Casco Bay), 30 Jul 1995, *Mathieson* (NHA # 57690), = drift specimens; Harpswell, Mark Island (Casco Bay), 6 Jul 2000, *Neefus & Shay* (NHA # 71756); Harpswell, Pond Island (Casco Bay), 6 Jul 2000, *Neefus & Shay* (NHA # 71754), with epiphytic *C. virgatum*; (NHA # 71755),



with epiphytic *Cystoclonium purpureum*; Harpswell, Ragged Island (Casco Bay), 6 Jul 2000, *Mathieson & Teasdale* (NHA # 71727–71729); Harpswell, Potts Point Cove, near old Harpswell Laboratory of Tufts University, 16 Sep 1999, *Mathieson* (NHA # 70016), with epiphytic *Ceramium virgatum* & *N. harveyi*; Harpswell, Potts Point, shoreline above old Harpswell Laboratory of Tufts University, 16 Sep 1999, *Hehre* (NHA # 69937, 69945), with epiphytic *N. harveyi*; (NHA # 69946), on *Fucus vesiculosus* var. *sphaerocarpus* with epiphytic *N. harveyi*; Harpswell, Basin Cove Falls, Potts Harbor (Casco Bay), 20 Feb 1995, *Mathieson & Hehre* (NHA # 54225); Harpswell, Basin Cove, opposite Peters Cove, 18 Sep 1999, *Mathieson* (NHA # 70231), = drift; Harpswell, Basin Point, near Dolphin Restaurant/Marina, Potts Harbor, 18 Sep 1999, *Mathieson* (NHA # 69923); Harpswell, tip of Ash Point Cove, lobster pound, Potts Harbor, 18 Sep 1999, *Mathieson* (NHA # 70646); Yarmouth, Doyle Point, Cousins Island (Casco Bay), 22 May 1995, *Mathieson* (NHA # 65149), = detached fragments with epiphytic *Ectocarpus fasciculatus*; Yarmouth, Little John Island, near Cousins Island, Talbot Rd. (Casco Bay), 31 Aug 1998, *Mathieson* (NHA # 67182); Long Island, South Beach, 13 May 2000, *Mathieson & Hehre* (NHA # 71718), = drift specimens; Portland, “The Bluffs”, Cliff Island (Casco Bay), 6 Oct 1998, *Hehre & Mathieson* (NHA # 67269); Portland, Stinky Beach, Cliff Island (Casco Bay), 15 Apr 2000, *Mathieson & Hehre* (NHA # 71726); Scarborough, Spurwink River Marsh near Higgins Beach, 6 Aug 1999, *Mathieson, Dawes & Hehre* (NHA # 70907); Scarborough, Pine Point Breakwater, mouth of Scarborough River, Saco Bay, 5 May 1995, *Mathieson* (NHA # 56201); Scarborough, Pine Point Breakwater, 28 Oct 1995, *True* (NHA # 59817), = drift specimen; Scarborough, Jones Creek, mouth of Scarborough Marsh (S side), 22 Jul 1998, *Mathieson & Dawes* (NHA # 69287), with epiphytic *N. harveyi*.

YORK CO: Old Orchard Beach, Stratton Island (NW side), Saco Bay, 9 Jun 1995, *Cook* (NHA # 59968); 15 Jun 1995, *Cook* (NHA # 59969); Old Orchard Beach, Little Stratton Island, 19 Jun 1995, *Cook* (NHA # 60048); Saco, Ferry Beach State Park, 3 May 1995, *Mathieson, Hehre & Cook* (NHA # 55249), = drift specimens; Biddeford, Biddeford Pool, 31 Mar 1996, *Mathieson* (NHA # 63022), with epiphytic *Neosiphonia harveyi*; 5 Jul 1997, *Mathieson* (NHA # 65345), with epiphytic *N. harveyi*; York, Nubble Light (Cape Neddick), 16 Nov 1989, *Mathieson* (NHA # 50042), growing in low tide pool with epiphytic *Sphacelaria cirrosa* and entangled *Chaetomorpha linum*, = first nearshore coastal record from southern Maine and New Hampshire; York, Long Sands Beach, 9 Jul 1994, *Hehre* (NHA # 51069), = drift specimens; York, Brave Boat Harbor Marsh, ~0.42 km inland from the Harbor’s mouth near old bridge pilings (in deep pannes), 16 Nov 1998, *Mathieson* (NHA # 68526–68527); Kittery, south bank of Brave Boat Harbor mouth, 23 Sep 1998, *Mathieson* (NHA # 68232), low tide pool; 24 Oct 1998, *Mathieson* (NHA # 68555), low tide pool; Kittery, Brave Boat Harbor Marsh, ~0.38 km inland from the Harbor’s mouth, just upstream from the outermost bridge pilings and near the mouth (W side) of a tributary delineating Cutts Island (in deep pannes), 19 Nov 1997, *Anderson* (NHA # 68302), with epiphytic *Ceramium virgatum*, *Berkeleya rutilans*, *Microco-*



*leus lyngbyaceus* & *Erythrotrichia carnea*; (NHA # 68582), with epiphytic *S. cirrosa* & *C. virgatum*; Kittery, Brave Boat Harbor Marsh, ~0.39 km inland from the Harbor's mouth on Cutts Island, near bridge pilings and the mouth of a major tidal tributary (in deep pannes), 21 Dec 1997, *Mathieson* (NHA # 67808); 11 Jan 1998, *Mathieson* (NHA # 66460); (NHA # 66467), with epiphytic *B. rutilans*; Kittery, Brave Boat Harbor Marsh, ~0.48 km inland from the Harbor's mouth on Cutts Island and behind a coastal berm (in deep pannes), 3 Dec 1997, *Mathieson* (NHA # 68028–68029), with epiphytic *S. cirrosa*; (NHA # 68031); Kittery, Seapoint, 19 Dec 1997, *Mathieson & Anderson* (NHA # 65973), with epiphytic *B. rutilans* & *N. harveyi*; Kittery, Sisters Point, Gerrish Island, 14 Mar 1998, *Mathieson* (NHA # 66782); Kittery, Fort Foster, Gerrish Island, 31 Jan 1998, *Smith, Harris & Wingate* (NHA # 66997).

ISLES OF SHOALS (ME): Kittery, Appledore Island, Babb's Cove near the Shoals Marine Laboratory, 7 Aug 1984, *Brady-Campbell* (NHA # 25897–25898), growing attached in shallow subtidal zone, with epiphytic *Neosiphonia harveyi*; exposed eastern side of island, 14 Oct 1993, *Stepenuck* (NHA # 50574), with epiphytic *N. harveyi*; exposed NE side, 17 Jun 2000, *Mathieson & Zechman* (NHA # 71720–71721, 71723–71724), with epiphytic *N. harveyi*, *Spongomorpha spinescens* & *Pilayella littoralis*; Kittery, Duck Island, Isles of Shoals, 2 Aug 1994, *Cook* (NHA # 52130); Kittery, Malaga Island, Isles of Shoals, 16 Aug 1994, *Pellitier & Cook* (NHA # 52133), with epiphytic *Ceramium virgatum*; Kittery, Smuttynose Island, Gosport Harbor side of Isles of Shoals, 29 Apr 1986, *Penniman* (NHA # 49343), with epiphytic *N. harveyi* & *Ulva lactuca*; = first occurrence beyond Babb's Cove (Appledore Island); 12 Aug 1994, *Totman* (NHA # 52132), with epiphytic *Trailliella intricata*; eastern (exposed) side of island, 3 Nov 1995, *Mathieson* (NHA # 60296).

#### NEW HAMPSHIRE

ISLES OF SHOALS (NH): Rye/Kittery, Gosport Harbor, 15 Jan 1997, *Harris* (NHA # 12519), SCUBA –20 ft., with epiphytic *Neosiphonia harveyi*; Rye, Lunging Island, Isles of Shoals, 14 Aug 1994, *Cook* (NHA # 52131); Rye, Seavey Island, Isles of Shoals, 16 Aug 1994, *Pellitier & Cook* (NHA # 52129); Rye, Star Island, Isles of Shoals, 15 Jan 1997, *Harris* (NHA # 12517), SCUBA –30 to –40 ft.; Rye, White Island, Isles of Shoals, 16 Aug 1994, *Pellitier & Cook* (NHA # 52128); 15 Jan 1997, *Harris* (NHA # 12508), SCUBA –20 to –30 ft., with epiphytic *N. harveyi*; 23 Aug 1997, *Harris* (NHA # 62092–62093), SCUBA –20 ft., drift and proliferous material, with entangled *Chaetomorpha picquotiana*.

NEARSHORE OPEN COAST, ROCKINGHAM CO: Newcastle, Jaffrey Point (Fort Stark), low tide pool, 14 Sep 1992, *Mathieson* (NHA # 50039), = first nearshore open coastal record from New Hampshire; 17 Feb 2000, low tide pool, *Kozuck & Beck* (NHA # 71418), with epiphytic *Polysiphonia fucoides*, *Titanoderma pustulatum*, *Ulva lactuca* & *Berkeleya rutilans*; Rye, Odiorne's Point, 5 Jun 1994, *Hehre* (NHA # 50779), = drift specimen; 18 Mar 1995, mid-tidal tide pool, *van Fleet* (NHA # 54355), = first attached material at the site; May 1995, *Cook* (NHA # 60115); 5 Dec 1999, low tide



pool, *Plummer* (NHA # 71552), with epiphytic *Neosiphonia harveyi*; Rye, North Wallis Sands, 3 Mar 1998, *Weymouth & Turnbull* (no specimen in NHA); Rye, Concord Point, 6 Feb 1998, *Wanat & Mayer* (NHA # 66792), in deep tide pool with epiphytic *N. harveyi*; Rye, Rye Ledge, 16 Oct 1985, *Zamojski* (NHA # 49072), = drift specimen; 30 Nov 1994, *Gerweck* (NHA # 52559), low tide pool, with epiphytic *N. harveyi*, = first attached material at the site; 5 Feb 2000, *Gunther, Hahn & Irwin* (NHA # 71108), with epiphytic *N. harveyi* & *Petalonia fascia*; North Hampton, Great Boar's Head, 1 Feb 1997, *Dick, Glaub & Jalbert* (no specimen in NHA).

GREAT BAY ESTUARY SYSTEM, ROCKINGHAM CO: Portsmouth, Inner South Mill Pond, 8 Jun 2001, *Mathieson & Grizzle* (NHA # 74346); *ibid.* (NHA # 74347–74349), with epiphytic *Neosiphonia harveyi*; Greenland, Week's Point, Great Bay, 6 Sep 1985, *Nelson* (NHA # 48860), = drift fragment entangled amongst *Zostera marina*.

HAMPTON-SEABROOK ESTUARY SYSTEM, ROCKINGHAM CO: Seabrook, mouth of creek between Knowles Island and mainland, 29 Jul 1998, *Mathieson & Dawes* (NHA # 69217–69218), with epiphytic *Neosiphonia harveyi*.

#### MASSACHUSETTS

ESSEX CO: Gloucester, Jones River town landing, Long Wharf, opposite Ram Island, 8 Aug 1998, *Mathieson* (NHA # 68490), with epiphytic *Neosiphonia harveyi*; Salem Harbor, Hawthorne Cove Marina, Salem, 8 Aug 2000, *Mathieson* (NHA # 72336); 14 Sep 2000, *Mathieson* (NHA # 72322).

NORFOLK CO: Cohasset, Cohasset Harbor Marsh, off Heatherly Rd., 21 Feb 1999, *Mathieson* (NHA # 69357), with epiphytic *Neosiphonia harveyi*, *Cladophora sericea*, *Melanosiphon intestinalis* & *Berkeleya rutilans*; (NHA # 69358).

PLYMOUTH CO: Scituate, off Driftway Rd. near mouth of North River, 21 Feb 1999, *Mathieson* (NHA # 69586); Plymouth, Gurnet Point, 23 Nov 1995, *North* (NHA # 59825).

BARNSTABLE CO: CAPE COD BAY, GULF OF MAINE: Barnstable, Barnstable Harbor, end of Bone Hill Rd., opposite Bone Point Light, 27 Mar 1999, *Mathieson* (NHA # 69518); Brewster, Quivett Creek Marsh, 1 Apr 2000, *Mathieson* (NHA # 71738), with epiphytic *Spermothamnion repens*; (NHA # 71739); Eastham, First Encounter Beach, end of Samoset Rd., 27 Mar 1999, *Mathieson* (NHA # 69537–69538), with epiphytic *S. repens*; (NHA # 69539), with epiphytic *Sphacelaria cirrosa*; Eastham, Coast Guard Beach, 1 Apr 2000, *Mathieson* (NHA # 71736–71737); Witchmere Harbor, 7 May 1966, *O'Brien* (NHA # 3106); South Wellfleet, Indian Neck, Wellfleet Harbor, 1 Apr 2000, *Mathieson* (NHA # 71733), with epiphytic *Sphacelaria cirrosa* & *S. repens*; South Wellfleet, Wellfleet Harbor, Old Wharf Rd., 27 Mar 1999, *Mathieson* (NHA # 69614); Provincetown, Provincetown Harbor, 4 Nov 2000, *Mathieson* (NHA # 73061–73062), with epiphytic *Ceramium virgatum*.